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Asteroids (Echinodermata) from the Campanian (Upper Cretaceous) rocky shore at Ivö Klack, southern Sweden

ANDREW SCOTT GALE

School of the Environment and Life Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO13QL, UK and Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK; e-mail: andy.gale@port.ac.uk

ABSTRACT:

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The asteroid fauna from the upper lower Campanian rocky coastline at Ivö Klack is described, and its palaeoecology is discussed in comparison with other Cretaceous and present-day shallow-marine assemblages. Twenty-six taxa are recorded, belonging predominantly to the Goniasteridae (11 species), with smaller representatives of the families Podosphaerasteridae (4 taxa), Astropectinidae (3 taxa), Forcipulatida (2 taxa), Pterasteridae, Korethrasteridae, Pseudarchasteridae, Pycinasteridae, Asterinidae, and Stauranderasteridae (all one species each). Five new genera are described (*Scaniasterina*, type species *S. surlyki* sp. nov.; *Granulasterias*, type species *G. ivoensis* sp. nov.; *Rugametopaster*, type species *Metopaster rugissimus* Gale, 1987a; *Ivoaster*, type species *I. soerensenae* sp. nov. and *Vectisaster*, type species *V. enigmaticus* sp. nov.). In addition, new species erected include *Astropecten erectus* sp. nov., *Manfredaster graveseni* sp. nov., *Metopaster asgaardae* sp. nov., *Nymphaster macrogranularis* sp. nov., *N. minigranularis* sp. nov., *Pycinaster christenseni* sp. nov. and *Remaster cretaceus* sp. nov. *Metopaster tamarae* Gale, 1987a, is transferred to the genus *Weitschataster* Neumann and Girod, 2018. The asteroid fauna shows marked similarities to a Cenomanian–Turonian assemblage from rocky shorelines in the Bohemian Basin, Czech Republic, but differs in important respects from present-day shallow-marine asteroid assemblages from around the world.

Key words: Asteroids; Campanian; rocky shoreline; Ivö Klack; Sweden.

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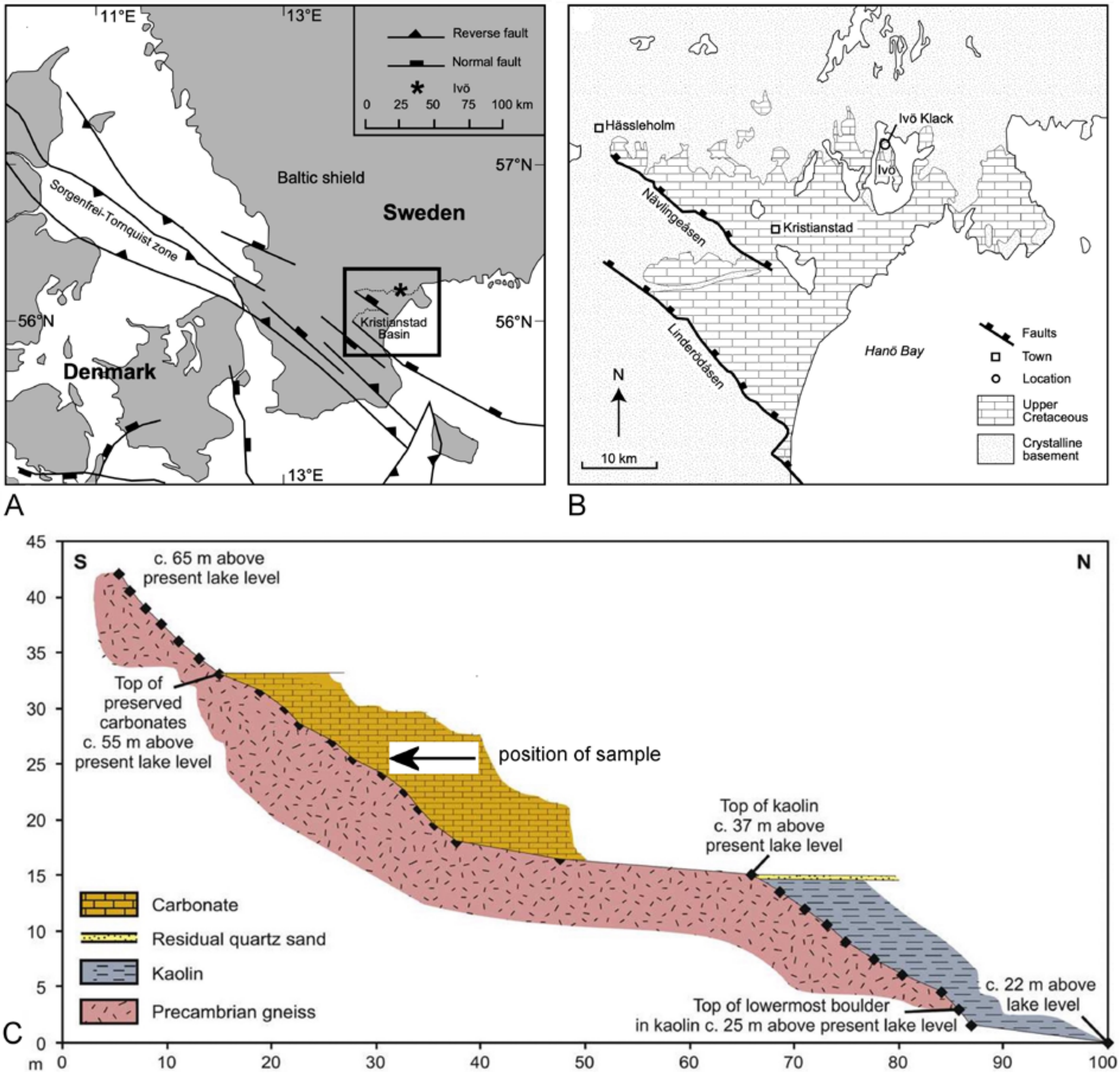
INTRODUCTION

The exposures at Ivö Klack in Skåne, southern Sweden (Text-fig. 1), provide a profile through a rocky shoreline of late early Campanian age (approximately 80 Ma), where boulders of Proterozoic gneiss were encrusted by zoned epifauna (Surlyk and Christensen 1974; Surlyk and Sørensen 2010), then buried by bioclastic shell sands and gravels composed of the calcitic remains of organisms, some of which lived on the boulders, and others in the surrounding carbonate sands and gravels. The locality probably represents a maximum water depth of 30 m, and among the diverse and abundant faunas (over 200 species), bryozoans, bivalves, echinoderms, serpulids and brachiopods were particularly abundant (Surlyk and Sørensen 2010; Sørensen and Surlyk 2010, 2011; Sørensen *et al.* 2011, 2012; Schrøder *et al.* 2018), as were cirripedes (Gale and Sørensen 2014, 2015).

A few goniasterid asteroids of the genus *Metopaster* Sladen, 1893 from Ivö Klack were described by Gale (1987a), who identified eight species. In 2011–2012 large samples were collected from a level approximately 10 m beneath the highest sedimen-



Text-fig. 1. Location of Ivö Klack. A – Map to show the position of the Kristianstad Basin in south-east Sweden; B – Kristianstad Basin with the position of Ivö Klack. C – Schematic cross-section through the Ivö Klack region to show the sedimentary facies and location of the large bulk sample (after Sørensen and Surlyk 2010, figs 2 and 6).

tary rocks preserved (Text-fig. 1C). Approximately 500 kg of soft sediment (hard pieces were discarded) were collected, washed and separated into fractions. All of the >3 mm fraction was picked, as well as approximately 1.5 kg of the 0.5–3 mm residue. In addition, a small portion of the 0.2–0.5 mm residue was picked. This represents about 200 hours of picking and yielded an estimated 1,500 asteroid and ophiuroid ossicles, which were sorted, identified and photographed using a USB microscope and SEM. The material was deposited in the collections of the Natural History Museum, Department of Palaeontology (NHMUK), London, UK.

The present paper offers systematic descriptions of the asteroid faunas from Ivö Klack and discusses their palaeoecology and occurrences in the light of known Cretaceous and present-day distributions of taxa.

A list of all the asteroid species known from Ivö Klack is presented in Table 1; these are described below under the systematic palaeontology section. Twenty-six asteroid taxa are identified, which is remarkably high for a rocky shore environment. The

Family	Genus, species	Mode of life	Species in basinal chalk	Genus in basinal chalk
Korethrasteridae	*Remaster cretaceus*	epifaunal	no	no
Pterasteridae	*Pteraster* cf. *cretachiton*	epifaunal, spongivore	yes	yes
Asterinidae	*Scaniasterina surlyki*	hard substrate feeder on epizoans/algae	no	no
Asteriidae	*Granulasterias ivoensis*	epifaunal, predator on molluscs	no	no
?Asteriidae		epifaunal, predator on molluscs	no	no
Pseudarchasteridae		?	no	no
Astropectinidae	*Astropecten erectus*	infaunal predator on invertebrates	no	yes
Astropectinidae	*Lophidiasterpygmaeus*	infaunal predator on invertebrates	yes	yes
Astropectinidae	*Coulonia* sp.	infaunal predator on invertebrates	?	?see Jagt (2000)
Goniasteridae	*Nymphaster minigranularis*	soft substrate predator?	no	yes
Goniasteridae	*Nymphaster macrogranularis*	soft substrate predator?	no	yes
Goniasteridae	*Metopaster calcar*	likely hard substrate dweller	no	yes
Goniasteridae	*Metopaster bromleyi*	likely hard substrate dweller	no	yes
Goniasteridae	*Metopaster elegans*	soft sediment dweller	no	yes
Goniasteridae	*Metopaster asgaardae*	?	no	yes
Goniasteridae	*Metopaster* sp. nov.	?	no	yes
Goniasteridae	*Weitschataster tamarae*	soft sediment dweller	no	yes
Goniasteridae	*Rugametopaster rugissimus*	hard substrate feeder on epizoans/algae	no	yes
Gomiasteridae	*Haccourtaster liticola*	hard substrate feeder on epizoans/algae	no	yes
Goniasteridae	*Ivoaster soerensenae*	?	no	no
Pycinasteridae	*Pycinaster christenseni*	soft substrate dweller?	no	yes
Stauranderasteridae	*Manfredaster graveseni*	soft substrate dweller?	no	yes
Podosphaerasteridae	*Valettaster argus*	associated with sponges?	yes	yes
Podosphaerasteridae	*Rugosphaeraster ruegenensis*	associated with sponges?	yes	yes
Podosphaerasteridae	*Vectisaster enigmaticus*	associated with sponges?	yes	yes
Podosphaerasteridae?		?	no	no

Table 1. The Ivö Klack asteroid fauna: family assignations, taxa, inferred mode of life, and occurrence in contemporaneous basinal chalks.

only comparable Cretaceous faunas, from the upper Cenomanian–lower Turonian of the Czech Republic (Žítt *et al*. 1997; Žítt 2004, 2005a, b), have not been fully described. The Ivö Klack asteroid assemblages, both in terms of diversity and abundance, are dominated by members of the family Goniasteridae, the large marginal ossicles of which are conspicuous fossils (Gale 1987a). However, careful screening of the finer (0.5–3 mm) residues has revealed a large diversity of asteroid taxa, including representatives of the families Korethrasteridae and Pterasteridae (Gale 2022a, b), as well as Pseudarchasteridae, Asteriidae, Asterinidae, Astropectinidae, Pycinasteridae, Stauranderasteridae and Podosphaerasteridae (Gale 2021). The nomenclature for asteroid ossicle description is taken from Gale (2011).

Institutional abbreviations:

BGS – British Geological Survey, Keyworth, Nottinghamshire, UK.
MMG – Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Dresden, Germany.
NHMUK – The Natural History Museum, London, UK.
SNSB – Bavarian State Collection of Palaeontology and Geology, Munich, Germany.

SYSTEMATIC PALAEONTOLOGY

Asteroidea de Blainville, 1830
Neoasteroidea Gale, 1987b
Order Velatida Perrier, 1884

DIAGNOSIS: Neoasteroids in which the actinal surface is constructed entirely from adambulacrals, which extend from the ambulacral grooves to the ambitus; actinal and marginal ossicles are absent (Gale 2018).

Korethrasteridae Danielssen and Koren, 1884

DIAGNOSIS: Velatids in which the adambulacrals broaden distally from articulation with the oral to the 3rd or 4th ossicle and possess an elongated adambulacral extension. The chevron-floored interradial grooves are open on the actinal surface (Gale 2018).

REMARKS: Korethrasterids comprise a small family of uncommon asteroids including two extant genera (*Peribolaster* Sladen, 1889, *Remaster* Perrier, 1894) and five living species. They form a paraphyletic sister group to pterasterids from both morphological and molecular studies (Mah and Foltz 2011; Gale 2018). Little is known about their modes of life.

Remaster Perrier, 1894

DIAGNOSIS: Small, arms short, abactinal plates cruciform, separated by large papular openings. Each plate bears a centrally placed cluster of divergent spines, united by a membranous web which forms an inverted cone.

TYPE SPECIES: *Korethraster palmatus* Perrier, 1894, by monotypy.

ASSIGNED SPECIES: In addition to the type species, *Remaster gourdoni* Koehler, 1912 and *Remaster cretaceus* sp. nov.

REMARKS: *Remaster* is a distinctive but uncommon asteroid at the present day, represented by two species: *R. gourdoni*, from the Falkland Islands (South Atlantic) and Antarctica, which occurs at depths between 10 and 540 m (Text-fig. 2A–E; Clark and Downey 1992) and *R. palmatus*, from the Caribbean, from Cuba to Brazil, occurring at depths between 298 and 421 m. The abactinal ossicles are highly distinctive, because they carry a central cluster of spine bases (Text-fig. 2D, E) to which the fascicles of spines attach. The oral ossicles are distinguished by a triangular oral body, bearing a fringe of oral spines and two suboral spines (Pl. 1, Fig. 18).

Remaster cretaceus sp. nov.
(Pl. 1, Figs 6–10, 16–18)

2022a. *Peribolaster* sp.; Gale, p. 5, fig. 8C–G.

DIAGNOSIS: *Remaster* in which the body of the oral ossicle is proportionately tall and the position of the actinal suboral spine is more abactinal. The insertion of the oral-adambulacral muscle is deep in the oral.

TYPES: The oral ossicle figured here (Pl. 1, Fig. 18) is the holotype (NHMUK PI EE 18258). The adambulacral ossicle (Pl. 1, Fig. 6; NHMUK PI EE 18259) and four abactinal ossicles (Pl. 1, Figs 7–10; NHMUK PI EE 18260–18263) are paratypes.

MATERIAL: Fifteen abactinal ossicles, one oral, one adambulacral and primary interradial.

DESCRIPTION: The abactinal ossicles (Pl. 1, Figs 7–10) are multilobed and individual lobes vary in size. Originally, the termination of the lobes under- or overlapped adjacent ossicles. The central region of the ossicles bears a ring of 4–5 low swellings (best seen in Pl. 1, Fig. 10) which in life carried the array of spines making up a fascicle (compare with Text-fig. 2D, E). The oral ossicle (Pl. 1, Fig. 18) has a robust, relatively high, triangular oral body, which has sites for the attachment of two suboral spines and a proximal fringe of about four oral spines. The site of insertion of the adambulacral-oral muscle is low and deep. The adambulacral is incomplete and worn (Pl. 1, Fig. 6), and the adambulacral extension is broken away; it carried four ambulacral spine bases.

REMARKS: The abactinal ossicles are assigned to *Remaster* on account of their irregularly cruciform outlines, slots for interabactinal articulations, and particularly the centrally placed cluster of rounded spine bases which bore a conical array of spines (compare Text-fig. 2D, E with Pl. 1, Figs 7–10). The oral ossicle (Pl. 1, Fig. 18) is similar in shape and spination to that of *Remaster gourdoni* (Text-fig. 2C; Pl. 1, Fig. 19), but the actinal suboral spine is more abactinal in position. The mode of life, substrates and diet of *Remaster* are unknown.

Pterasteridae Perrier, 1875

DIAGNOSIS: Velatida in which the primary radial ossicles carry a vase-shaped pedicel and the other abactinals a tall, cylindrical pedicel. Muscles are present between abactinals and abactinal-chevron ossicle contacts (Gale 2018).

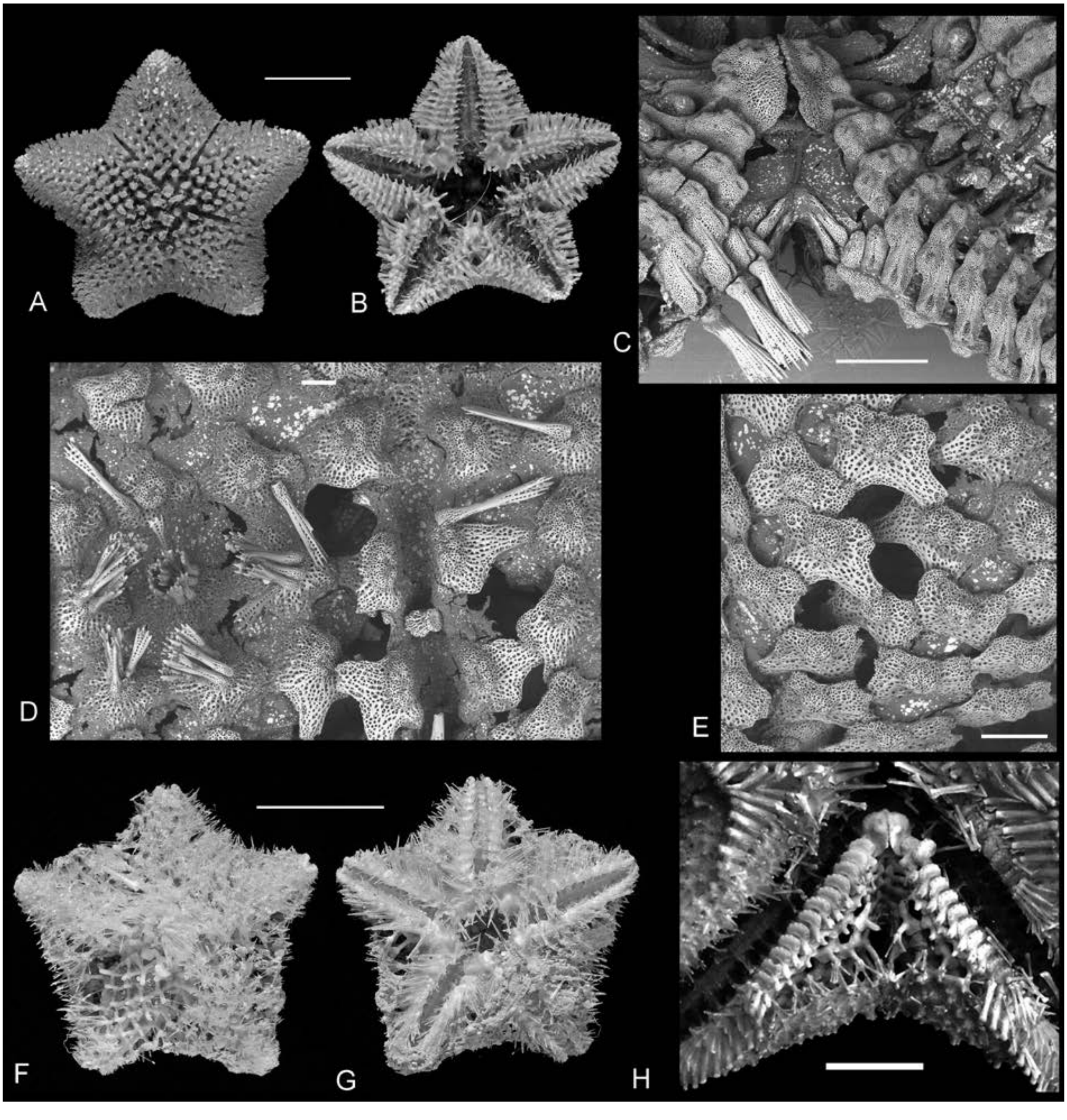
REMARKS: The pterasterid skeleton is very lightly constructed (Text-fig. 2F, G) and disintegrates rapidly after death. However, the adambulactal and abactinal ossicles are highly distinctive (Text-fig. 2H). Pterasterids have an extensive fossil record, ranging from the Middle Jurassic (Bajocian) to the present day (Gale 2018). Isolated ossicles of the genus *Pteraster* are present, but uncommon, in Upper Cretaceous chalks of northwest Europe, from which nine species have been described (Gale 2022a, b). These are characterised by features of the adambulacral ossicles and demonstrate the presence of four lineages extending from the Cretaceous to the present day.

Pteraster cf. *cretachiton* Gale, 2022a
(Pl. 1, Figs 2, 3, 11, 12, 15)

2022a. *Pteraster* cf. *cretachiton* Gale, p. 15, fig. 8A, H, I, K.

MATERIAL: Ten abactinal ossicles, five ambulacrals and one adambulacral from the upper lower Campanian of Ivö Klack (NHMUK).

DESCRIPTION: The ambulacral ossicles (Pl. 1, Figs 2, 3) can be distinguished by the elongated process on the proximal part of the ambulacral head, the short distal process and the tall dentition. A single adambulacral ossicle (Pl. 1, Fig. 15) is present. Pterasterid adambulacrals are taxonomically useful and are amongst the most distinctive of all asteroid ossicles, and their complex morphology reflects their function as part



Text-fig. 2. Selected velatids. A–E – *Remaster gourdoni* Koehler, 1912; A, B – individual in abactinal and actinal views, respectively; C – enlargement of partly denuded actinal interradial region; D, E – partly denuded and mostly denuded abactinal surfaces, respectively. F, G – *Pteraster acicula* (Downey, 1970), in abactinal and actinal views, respectively. H – *Pteraster pulvillus* Sladen, 1889, partly denuded actinal interradial region. Provenance: A–E are from the Falkland Islands, south Atlantic; F, G is from the Caribbean; H is from the North Atlantic. Scale bars equal 10 mm (A, B, F–H) and 0.2 mm (C–E).

of the specialised respiratory apparatus (Gale 2018, 2022a). They consist of a flattened, suboval adambulacral flange which strongly imbricates the adjacent plates; the abradial portion of the ossicle comprises an adambulacral extension of which the distal terminations articulate with the long, webbed actinolateral spines (Text-fig. 2H). The single adambulacral from Ivö Klack is comparable in shape with that of *P. cretachiton* (Pl. 1, Fig. 14) but is insufficiently well preserved to be certain that it belongs to that species. The abactinal ossicles, called megapaxillae (Pl. 1, Figs 11, 12) have a four- or multilobed base from which a tall, columnar pedicel with a rounded cross-section arises; these pedicels support the muscular canopy which surrounds the pterasterid body (Text-fig. 2F–H).

REMARKS: Pterasterids are a predominantly deep-sea (bathyal and abyssal) family at the present day, but two species extend into shallow water; *Pteraster tesselatus* Ives, 1888, from the northeast Pacific which dwells on rocky substrata in depths of 5 to 590 m (Lambert 2000), and the circumboreal *P. militaris* (O.F. Müller, 1776), which ranges from 10 to 1,100 m (Clark and Downey 1992). *Pteraster tesselatus* feeds mainly on sponges, ascidians and bivalves (Jangoux 1982).

Forcipulatida Perrier, 1884

DIAGNOSIS: Asteroids with a small, well-defined disc and long arms. They possess forcipulate pedicellariae, which include a basal piece and a muscular stalk.

REMARKS: Forcipulatida are a well-demarcated group of neoasteroids which appeared suddenly in the Early Jurassic and are abundant and diverse at the present day (Fau et al. 2024).

Asteriidae Gray, 1840

DIAGNOSIS: Forcipulatida in which specialised clusters of crossed pedicellariae are present around primary spines (wreath organs); abactinal skeleton reticulate, adoral carina present, four rows of tube feet; keyhole pustules present on inferomarginals (modified from Fau and Villier 2020).

REMARKS: In a detailed cladistic investigation of forcipulatid relationships, Fau and Villier (2020) characterised the Asteriidae by the presence of wreath organs (clusters of crossed pedicellariae which move up and down primary spines), a reticulate skeleton, the presence of an adoral carina, and four rows of tube feet. Additionally, they noted that all asteriids have only slit-like spine bases on the inferomarginals which they referred to as keyhole pustules or *psas* (Fau and Villier 2020, p. 8; Fau *et al.* 2024, pp. 27, 36). Wreath organs are only known in a single fossil taxon, the Maastrichtian *Cretasterias reticulatus* Gale and Villier, 2013, which does not possess keyhole pustules on the inferomarginals (Fau *et al*. 2024) and was therefore considered to belong probably to the stem group of the Asteriidae. Identification of isolated fossil ossicles of forcipulatid affinity is clearly fraught with problems, and taxa such as *Savignasterias villieri* Gale, 2011 should be considered as Forcipulatida *incertae sedis* (Fau *et al*. 2024). However, I consider that isolated ossicles still have considerable potential for understanding forcipulatid evolution, especially when large numbers of ossicles of a single taxon are available, as at Ivö Klack.

Granulasterias gen. nov.

DIAGNOSIS: Inferomarginals tear-drop shaped, each carrying two slit-like spine bases on the actinal margin. All external ossicles bear a region of closely spaced rugosities linked by fine struts.

TYPE SPECIES: *Granulasterias ivoensis* gen. et sp. nov.

DERIVATION OF NAME: In reference to the presence of rugosities on the ossicles.

REMARKS: *Granulasterias* gen. nov. is referred to the Asteriidae on the presence of only keyhole pustules (elongated spine bases) on the inferomarginals, a synapomorphy of the family (Fau and Villier 2020, p. 8).

Granulasterias ivoensis gen. et sp. nov.
(Pl. 2, Figs 1–10, 12–14)

DIAGNOSIS: As for genus.

TYPES: The inferomarginal ossicle illustrated in Pl. 2, Fig. 8 is the holotype (NHMUK PI EE 18264). The other figured ossicles are paratypes (NHMUK PI EE 18265, 18276), all from the upper lower Campanian at Ivö Klack.

MATERIAL: Over 200 dissociated ossicles, including abactinals and marginals from the type locality.

DERIVATION OF NAME: After Ivö Klack, the type locality.

DESCRIPTION: Inferomarginals (Pl. 2, Figs 8–10) tear-drop shaped, central area slightly concave, bearing closely paced rugosities. Actinal margin convex, with two vertically oriented, slit-like spine bases (keyhole pustules). Superomarginals (Pl. 2, Figs 3–5) cruciform, abactinal process longer than actinal or lateral ones, central region rugose. Abactinals of uncertain position (Pl. 2, Figs 1, 2, 12) triangular, rugose. Radial ossicles (Pl. 2, Figs 6, 7) symmetrical, rhombic to cruciform, distal portion bearing a large, circular spine base. Abactinal ossicle from disc (Pl. 2, Fig. 13) pentagonal, central region slightly depressed. Madreporite (Pl. 2, Fig. 14) fused with adjacent abactinal ossicles.

REMARKS: This species is common in finer residues from Ivö Klack. The millimetric ossicles indicate a small body size with an arm length of a few centimetres. Asteriids at the present day are predators and scavengers on invertebrates (Jangoux 1982).

Asteriid or stichasterid
(Pl. 2, Figs 11, 15–17)

MATERIAL: Twenty radial and marginal ossicles.

DESCRIPTION: Radials cruciform (Pl. 2, Figs 15–17), imbricating proximally, lacking rugosities, with a single rounded spine base on proximal part of abactinal surface. Superomarginals (Pl. 2, Fig. 11) also cruciform, elongated, with centrally placed spine base.

REMARKS: Although these ossicles probably belong to a single species of small forcipulate, the material is insufficient for more precise placement within the group.

Forcipulatida *incertae sedis*
(Pl. 2, Figs 18–21)

MATERIAL: Thirty-five ambulacral ossicles, two circumoral and one oral ossicles from Ivö Klack.

REMARKS: These ossicles evidently belong to forcipulate asteroids but have insufficient features to be placed in lower-rank taxonomic groups.

Valvatacea Blake, 1987
Valvatida Perrier, 1884
Asterinidae Gray, 1840

DIAGNOSIS: Body pentagonal to stellate, convex abactinally, concave actinally. Abactinal ossicles imbricated, marginal plates small, inconspicuous, often indistinguishable from abactinals and actinals (modified from Clark and Downey 1992).

REMARKS: The Asterinidae are morphologically very variable (Clark and Downey 1992), but molecular analysis indicates their monophyly (Mah and Foltz 2011). Most extant taxa live on hard substrates in relatively shallow water, feeding by stomach extrusion on epifauna (Jangoux 1982). The fossil record of asterinids is very poor, being confined to the Middle Jurassic tremasterines (Gale 2018). This may perhaps reflect on the scarcity of fossil asteroids in shallow-water deposits associated with hard substrates.

Scaniasterina gen. nov.

DIAGNOSIS: An asterinid with large, robust, proximally imbricating abactinal ossicles, the distal margin of which bear a crest of 15–20 short processes which probably bore spines. Actinal ossicles robust, strongly imbricated, with rounded spine pits on distal surface.

TYPE SPECIES: *Scaniasterina surlyki* gen. et sp. nov.

REMARKS: Proximally imbricating abactinal ossicles are characteristic of many asterinid species, the general morphology of which is illustrated here by the extant *Stegnaster inflatus* (Pl. 3, Figs 11, 12). The ossicles of *Scaniasterina* gen. nov. are remarkably similar in arrangement to those of the living, deep-water, hard substrate-dwelling asterinid *Tremaster mirabilis* Verrill, 1879 (Pl. 3, Figs 10, 13), in shape and pattern of imbrication. However, in *T. mirabilis* the external surfaces of the ossicles are constructed of shiny, imperforate stereom, rather than the dense, layered stereom of *Scaniasterina* gen. nov. Additionally, *T. mirabilis* lacks the distal crest present in *Scaniasterina* gen. nov. An undescribed species of the new genus is present in the lower Turonian of Velim, Czech Republic (pers. obs.).

Scaniasterina surlyki gen. et sp. nov.
(Pl. 3, Figs 1–9)

DIAGNOSIS: As for genus.

TYPES: The abactinal ossicle figured here (Pl. 3, Fig. 1) is holotype (NHMUK PI EE 18277). The other figured ossicles are paratypes (NHMUK PI EE 18278–18285), all from the upper lower Campanian at Ivö Klack.

MATERIAL: Thirty-eight ossicles from the type locality.

DERIVATION OF NAME: For Finn Surlyk, who has pioneered and led research into the Ivö Klack site and its faunas.

DESCRIPTION: All ossicles are distinguished by the fact that the external surface is very white and porous, whereas the remainder of the ossicle is yellow and solid. The abactinal ossicles (Pl. 3, Figs 1–3) are robust, subrectangular to rhombic in outline; radial ossicles (Pl. 3, Fig. 1) are bilaterally symmetrical and relatively weakly imbricated, forming a single column, whereas those from interradial positions (Pl. 3, Figs 2, 3) formed alternating columns. The distal margin of the abactinals bears a crest made up of 15–20 short processes, and a centrally placed, circular spine pit is present proximal to this (Pl. 3, Figs 1, 2). The external surface of the abactinals bears fine, shallow spine pits (e.g., Pl. 3, Fig. 2, right-hand side), but these have been removed by abrasion on most specimens (e.g., Pl. 3, Fig. 3). Ossicles interpreted to be actinals (Pl. 3, Figs 4–9) are variable in shape, imbricated strongly, and have a relatively small external surface which bears large, circular spine pits.

REMARKS: It is noteworthy that there is significant abrasion on the outer (exposed) surfaces of some of the abactinals (e.g., Pl. 3, Figs 2, 3) which is not present on the portions of the ossicles which would have been protected because they were covered by the imbricating adjacent plates. This could be interpreted to indicate that this species lived in a very high-energy environment, perhaps on the surface of boulders, where abrasion would have been considerable.

Paxillosida Perrier, 1884
Astropectinidae Gray, 1840

DIAGNOSIS: Five-armed, flattened paxillosids, possessing broad marginal frame made up of paired, opposing, supero- and inferomarginals; fascioles running abactinally-actinally between individual supero- and inferomarginal pairs in majority of genera; abactinal surface composed of small paxillae; actinals, when present, in well-defined rows of imbricating plates (modified from Clark and Downey 1992).

INCLUDED GENERA: WoRMS currently lists 37 genera of Astropectinidae (https://www.marinespecies.org at VLIZ. Accessed 2024-11-11. doi:10.14284/170).

REMARKS: Assignation of Late Cretaceous astropectinids to genera has proved to be very difficult. Material has mostly been placed in *Lophidiaster* Spencer, 1913 (type species *L. ornatus* Spencer, 1913), but the holotype of the type species is indeterminable (Gale 1988) and is now lost; Jagt (2000) suggested that type species status for *Lophidiaster* should be transferred to *L. pygmaeus* Spencer, 1913, which is a well-defined species. *Spenceraster* Lambert, 1914 (type species *Nymphaster rugosus* Spencer, 1905) has generally been assigned to the Goniasteridae (Spencer and Wright 1966) but is actually an astropectinid. Many Cretaceous astropectinids have been referred to *Coulonia* de Loriol, 1874 (see Jagt 2000; Gale 2020a; Ewin and Gale 2020; Gale *et al*. 2024).

Lophidiaster Spencer, 1913

Lophidiaster pygmaeus Spencer, 1913
(Pl. 3, Figs 19–21)

1913. *Lophidiaster pygmaeus* Spencer, pp. 139, 150, pl. 11, fig. 20, pl. 16, figs 17–19.
1950. *Astropecten? pygmaeus* (Spencer); Rasmussen, p. 92, pl. 10, fig. 19.
1956. *Lophidiaster pygmaeus* Spencer; A.H. Müller, p. 642, pls 1, 2.
2000. *Lophidiaster pygmaeus* Spencer; Jagt, p. 391, pl. 4, figs 1–7.
2023. aff. *Lophidiaster*; Neumann *et al*., p. 484, fig. 5A–D.

DIAGNOSIS: A small species in which the superomarginals bear a cluster of rounded rugosities on their abactinal surface.

TYPES: Syntypes are marginal ossicles (NHMUK PI EE 13263, 13264) from the lower Maastrichtian of Rügen, northeast Germany.

MATERIAL: Six superomarginals from Ivö Klack, upper lower Campanian.

REMARKS: The Ivö Klack marginals agree in detail with marginals of this species figured by previous authors. The species occurs widely in the basinal Campanian and Maastrichtian chalks of northwest Europe. Kutscher (2013, fig. 2) illustrated an articulated specimen of *L. pygmaeus* in a flint from Rügen which shows the body form of the species. The interradii are broad and evenly concave and the marginal frame is robust.

Astropecten Gray, 1840

DIAGNOSIS: Intermarginal facets small, intermarginal fascioles broad, deep; superomarginals smaller than inferomarginals. Inferomarginals bearing horseshoe-shaped spine bases, superomarginals with smaller spines. Actinal interareas small.

TYPE SPECIES: *Asterias aranciaca* Linnæus, 1758, by the subsequent designation of Fisher (1908).

REMARKS: At the present day, *Astropecten* is a diverse (over 150 species) and well-defined genus, from both molecular and morphological studies, as demonstrated by Zulliger and Lessios (2010). The use of the generic name for fossil species is more problematical, because it has been used as a sack genus for many extant forms, without consideration of the precise morphological diagnosis of the genus. Marginal ossicles of extant *Astropecten* are actually quite distinctive, as shown by Blake (1973, pl. 14); the interradial superomarginals are upright, with a triangular intermarginal articular surface and broad intermarginal fascioles. The interradial inferomarginals have an angled intermarginal articulation and intermarginal fascioles which broaden towards the ambitus. Using these criteria, species from the Paleogene of northwest Europe described by Rasmussen (1972; *A. postornatus* Rasmussen, 1945 and *Astropecten granulatus* Rasmussen, 1972) appear to be correctly placed. The same holds true for some astropectinid marginals referred to *Astropecten* by Jagt (2000, pl. 2, figs 7, 8).

Astropecten erectus sp. nov.
(Pl. 3, Figs 15–18)

part 2000. goniasterid? sp. 4; Jagt, p. 426, pl. 1, fig. 6; pl. 2, figs 9, 10 only.

DIAGNOSIS: *Astropecten* in which the interradial inferomarginals are tall and upright and bear only one or two large spine bases on the external face.

TYPE: The median inferomarginal figured (Pl. 3, Figs 15, 18) is holotype (NHMUK PI EE 18286). The other figured inferomarginals are paratypes (NHMUK PI EE 18287–18289), all from the upper lower Campanian at Ivö Klack.

MATERIAL: Eight inferomarginal ossicles from the type locality.

DERIVATION OF NAME: Latin *erectus*, meaning upright, in reference to the shape of the median inferomarginals.

DESCRIPTION: Interradial inferomarginals (Pl. 3, Figs 17, 18) are narrow and tall (height 2.5× breadth) and the external margin is slightly convex and nearly vertical. A strong articular ridge separates the articulation with the adjacent ossicle from a broad fasciolar surface. The external surface bears two large spine bases. Inferomarginals of more distal positions (Pl. 3, Figs 15, 16) are broader and appear to carry more spine bases.

REMARKS: This material, and that of Jagt (2000, pl. 1, fig. 6; pl. 2, figs 9, 10), which is of late Maastrichtian age, is distinctive on account of the very tall interradial inferomarginals which bear only one or two large spine bases. The generic assignation is provisional.

Coulonia de Loriol, 1874

DIAGNOSIS: Astropectinids with a broad disc and relatively short arms, actinal interradii very broad. Marginals short and broad, tapering slightly towards lateral margin and possessing very deep intermarginal fascioles. Inferomarginals broader than superomarginals and bearing transversely arranged coarse spine pits. Superomarginals with regularly spaced pits for short, blunt spines (Ewin and Gale 2020).

TYPE SPECIES: *Coulonia neocomensis* de Loriol, 1874, by monotypy.

REMARKS: *Coulonia* is a very well-defined genus which is characteristic of relatively shallow-marine habitats in the Cretaceous (Ewin and Gale 2020). Jagt (2000) recorded typical marginal ossicles from the upper Campanian and Maastrichtian of the Netherlands and northreast Belgium.

Coulonia sp.
(Pl. 3, Figs 22–25)

MATERIAL: Four superomarginals from the upper lower Campanian, Ivö Klack, southern Sweden.

DESCRIPTION: The superomarginals are rectangular in abactinal view and possess sharply defined articulation structures, comprising a narrow, curved ridge and a short process close to the intermarginal facet. The intermarginal fascioles are moderately deep. The abactinal surface is slightly convex, bearing an even covering of spine pits.

REMARKS: The evenly spaced spine pits on the superomarginals and rather flat abactinal surface are typical of *Coulonia*.

Pseudarchasteridae Sladen, 1889

DIAGNOSIS: Paxillosid asteroids which possess a marginal frame carrying shallow intermarginal fascioles; tube feet with a flattened termination; oral ossicle pairs with a single, proximally directed spine in each interradius.

INCLUDED GENERA: *Paragonaster* Sladen, 1889; *Pseudarchaster* Sladen, 1889; *Perissogonaster* Fisher, 1913; *Gephyreaster* Fisher, 1910; *Comptonia* Gray, 1840; *Sucia* Blake, 1973.

REMARKS: Pseudarchasterinae, as a subfamily, were long considered to belong with the Goniasteridae, or not even recognised as a discrete subfamily (Clark and Downey 1992). Molecular analysis has demonstrated that they should be placed within the Paxillosida (Mah and Foltz 2011), which accords with a number of morphological features such as the presence of shallow intermarginal fascioles and rudimentary pedicellariae.

?Pseudarchasteridae
(Pl. 4, Fig. 17)

MATERIAL: A single median superomarginal ossicle (NHMUK PI EE 18298).

DESCRIPTION: The abraded superomarginal is short and broad, and wedges to an acutely angled lateral margin. The abactinal margin is weakly domed, and an intermarginal fasciole of even breadth is present. The abactinal surface is smooth.

REMARKS: This ossicle is provisionally referred to the Pseudarchasteridae on account of the narrow intermarginal fasciole which is of even breadth. In astropectinid superomarginals (e.g., Pl. 3, Figs 13, 14, 24, 25) the intermarginal articular surfaces are more sharply defined and raised.

Goniasteridae Forbes, 1841

DIAGNOSIS: Body flat, distal arms sometimes raised abactinally. Disc proportionately broad, large, opposing supero- and inferomarginals. Abactinal surface formed of tessellation of tabular to paxilliform ossicles (Gale 1987a).

REMARKS: This is a large and very diverse family, including over 120 genera (https://www.marinespecies.org at VLIZ. Accessed 2024-11-11. doi:10.14284/170), which appears to be monophyletic on the basis of molecular analyses (Mah and Foltz 2011). Goniasterids first appeared in the Early Jurassic and persist to the present day.

Nymphaster Sladen, 1889

DIAGNOSIS: Arms long, narrow, well demarcated from disc; superomarginals meeting over radius. Abactinal ossicles tall, polygonal. All ossicles bearing covering of granular or short conical spines. Pedicellarial attachment area comprising central cavity with raised rim flanked by two triangular grooves.

TYPE SPECIES: *Nymphaster protentus* Sladen, 1889, by the subsequent designation of Fisher (1919).

REMARKS: Numerous species of *Nymphaster* have been described from the Cretaceous (e.g., Gale 1987c; Breton 1992; Jagt 2000; Jagt *et al*. 2021).

Nymphaster minigranularis sp. nov.
(Pl. 4, Figs 8–11, 14–16)

DIAGNOSIS: Marginal ossicles with dense cover of very fine, shallow, closely spaced rounded granule pits.

TYPE: The inferomarginal figured in Pl. 4, Fig. 11 is the holotype (NHMUK PI EE 18291). The other figured ossicles are paratypes (NHMUK PI EE 18292–18298), all from the upper lower Campanian at Ivö Klack.

MATERIAL: Over 150 marginal ossicles from the upper lower Campanian of Ivö Klack.

DERIVATION OF NAME: With reference to the very fine granule pits which cover the external faces of marginal ossicles.

DESCRIPTION: Marginals short and broad (breadth up to four times length), rectangular in actinal/abactinal view. Interradial superomarginals (Pl. 4, Figs 8 upper and 9) low, with external face angled at 45º to the intermarginal suture, external face gently convex. Median inferomarginals (Pl. 4, Figs 8 lower, 10 and 11) with evenly convex outer face, no separation of actinal and lateral surfaces. Proximal superomarginals of arm (Pl. 4, Figs 14, 15) taper distally. External faces of all marginals completely covered by fine, dense granule pits, pedicellariae absent.

REMARKS: This species is referred to *Nymphaster* on the block-like form of the marginal ossicles which have an even, dense covering of granular spine pits. Pedicellariae have not been found, and the arms were relatively poorly demarcated from the disc, as the material does not comprise any "angle" ossicles marking the boundary between the disc and the arms (see Gale 1987c).

Nymphaster macrogranularis sp. nov.
(Pl. 4, Figs 1–7, 12, 13)

DIAGNOSIS: *Nymphaster* with evenly convex outer faces of marginals bearing coarse, evenly spaced, deeply impressed granule pits.

TYPE: The superomarginal ossicle illustrated in Pl. 4, Fig. 2 is the holotype (NHMUK PI EE 18299). The other figured ossicles are paratypes (NHMUK PI EE 18300–18307), all from the upper lower Campanian at Ivö Klack.

MATERIAL: 112 isolated marginal ossicles from the same locality as the type material.

DESCRIPTION: The median marginals (Pl. 4, Figs 1–3) are narrow and broad (breadth approximately 4× length) and rectangular in actinal/abactinal view or tapering slightly towards lateral margin (Pl. 4, Figs 6, 7). The superomarginals (Pl. 4, Fig. 1 upper, Pl. 6, Fig. 2) are evenly and gently convex, and the outer face is angled at 45º to the intermarginal suture. In large superomarginals, the abactinal part of the outer face is weakly tumid (Pl. 4, Figs 6, 7). The median inferomarginals (Pl. 4, Fig. 1 lower, Pl. 6, Fig. 3). Distally, the marginals narrow (Pl. 4, Figs 4, 5, 13) and the weak intermarginal grooves become more prominent. The external faces of all marginals bear coarse, densely spaced, impressed granule pits.

REMARKS: *Nymphaster macrogranularis* sp. nov. may be consistently separated from *N. minigranularis* sp. nov. (see above) by the coarser, more deeply impressed granule pits on the marginal ossicles.

Metopaster Sladen, 1893

DIAGNOSIS: Outline pentagonal, sides slightly concave, straight to slightly convex. Marginal border broad, made up of relatively few square to rectangular marginals and a triangular ultimate superomarginal which corresponds with 1 to 7 inferomarginals (Gale 1987a).

TYPE SPECIES: *Goniaster* (*Goniodiscus*) *parkinsoni* Forbes, 1848, by subsequent diagnosis of Rasmussen (1950).

REMARKS: Over 50 Cretaceous and Paleocene species have been assigned to *Metopaster* (see Rasmussen 1950; Schulz and Weitschat 1971, 1975; Breton 1992; Gale 1987a, 1989; Jagt 2000). Recently, two species have been reassigned to *Weitschataster* Neumann and Girod, 2018, i.e., *M. undulatus* Spencer, 1913 and *M. decipiens* Spencer, 1913. Herein I place *Metopaster tamarae* Gale, 1987a in this genus as well. *Rugasphaeraster* gen. nov. is erected for *Metopaster rugissimus* Gale, 1987a. Possible undescribed forms of *Metopaster* are found at the present day in the Philippines region of the Indo-Pacific (Pl. 6, Figs 1, 2).

Metopaster calcar Spencer, 1913
(Pl. 5, Figs 8–15)

part 1913. *Metopaster calcar* Spencer, p. 119, pl. 15, figs 12, 14–16 only.
1987a. *Metopaster calcar* Spencer; Gale, p. 24, pl. 8, figs 12–21.

DIAGNOSIS: Ultimate superomarginal elongated, bearing abactinally directed, blunt, rounded protuberances. Granule pits restricted to abactinal processes.

TYPE: The ultimate superomarginal figured by Spencer (1913, pl. 15, figs 14–16) was designated lectotype by Gale (1987a, p. 24). It is from the upper lower Campanian of Balsberg, southern Sweden (NHMUK PI EE 13305).

MATERIAL: An estimated 1,500 isolated marginal ossicles from Ivö Klack, 50 marginals from Ignaberga (both upper lower Campanian), and 15 marginals from Ringelslät (Santonian), all in southern Sweden.

REMARKS: This is the most common asteroid at Ivö Klack and the morphology of the superomarginals shows considerable morphological variation, illustrated previously by Gale (1987a, pl. 8, figs 12–21).

Metopaster bromleyi Gale, 1987a
(Pl. 6, Figs 23–26)

part 1913. *Metopaster parkinsoni,* var. *calcar* Spencer, pp. 119, 120, pl. 15, fig. 13 only.
1987a. *Metopaster bromleyi* Gale, p. 22, pl. 2, figs 11–13; pl. 3, figs 1–5.

DIAGNOSIS: Marginals with a narrow, depressed border, central area bearing large, shallow, round granule pits, the ultimate superomarginal carrying two conical projections, the more proximal one directed abactinally, the distal abactinolaterally.

TYPES: An ultimate supromarginal from Ivö Klack, southern Sweden, is the holotype (NHMUK PI EE 13304), and marginals from the same locality are paratypes (NHMUK PI EE 54192–54193), all from the upper lower Campanian.

MATERIAL: Over 100 marginals from the upper lower Campanian of Ivö Klack.

REMARKS: *Metopaster bromleyi* appears most closely related to the Cenomanian–Turonian species *M. thoracifer* (Geinitz, 1872), but differs in its possession of an abactinally directed process on the ultimate superomarginal, absent in *M. thoracifer.* Breton (1992, figs 46, 168) identified intermediate forms from the Coniacian–Santonian of France. *Metopaster bromleyi* is present, but not abundant, in the upper lower Campanian of Ivö Klack, Balsberg and Ignaberga in southern Sweden.

Metopaster elegans Gale, 1987a
(Pl. 5, Figs 5–7)

1987a. *Metopaster elegans* Gale, p. 28, pl. 8, fig. 24; pl. 9, figs 1–3.

DIAGNOSIS: External surfaces of all marginals covered with dense, fine granule pits; central area absent. The ultimate superomarginal is long and narrow with a large, vertical, lateral face and a narrow, convex abactinal surface. Median marginals with slanted distal surfaces.

TYPE: The ultimate superomarginal figured by Gale (1987a, pl. 9, fig. 1) is the holotype (NHMUK PI EE 54274). The other ossicles figured are paratypes (NHMUK PI EE 54273, 54275, 54276). All are from the upper lower Campanian at Ivö Klack, southern Sweden.

MATERIAL: 75 isolated marginals from the type locality.

REMARKS: This species is common at Ivö Klack and is also present at Ignaberga in the upper lower Campanian.

Metopaster asgaardae sp. nov.
(Pl. 5, Figs 1–4)

DIAGNOSIS: Superomarginal with cover of sparse, rather widely spaced granule pits in well-defined central area; abactinal and lateral surfaces confluent, evenly arched. Ultimate superomarginal with length twice breadth, distal abactinal part elevated.

TYPE: The ultimate superomarginal figured (Pl. 5, Figs 1, 2) is the holotype (NHMUK PI EE 18308). The median superomarginal figured (Pl. 5, Figs 3, 4) is a paratype (NHMUK PI EE 18309), both from the upper lower Campanian at Ivö Klack.

MATERIAL: A further five ultimate superomarginals and two median superomarginals from the same locality (NHMUK, A.S. Gale Collection).

DERIVATION OF NAME: For the late Ulla Asgaard, in recognition of her work on brachiopods and echinoids.

DESCRIPTION: Breadth of median superomarginals (Pl. 5, Figs 3, 4) greater than length, with narrow depressed border and sharply defined central area which bears widely spaced, shallow, round granule pits. External surface evenly convex, lateral and abactinal surfaces confluent. The ultimate superomarginal (Pl. 5, Figs 1, 2) is triangular in abactinal view, length twice breadth, external surface evenly convex, bearing even cover of granule pits. In lateral view, the distal portion of the ossicle is elevated and corresponds with 4–5 inferomarginals, the most distal of which was almost vertical in orientation.

REMARKS: In abactinal view, the ultimate superomarginal is similar in shape to that of *Metopaster polyplacus* Schulz and Weitschat (1971, pl. 23, figs 7, 9), but becomes elevated distally such that the ultimate inferomarginal is nearly vertical in orientation. Additionally, the median superomarginals are broader than long, whereas they are nearly square in *M. polyplacus* (see also Neumann *et al.* 2023, fig. 11). *Metopaster asgaardae* sp. nov. differs from *Metopaster* sp. 3 of Jagt (2000, pl. 12, figs 18, 19) in that the sculpture comprises widely spaced, shallow granule pits on a smooth surface, rather than closely spaced, fine pits.

Metopaster sp. nov.

1987a. *Metopaster* sp. nov. Gale, p. 43, pl. 8, fig. 23.

MATERIAL: A single median superomarginal from Ivö Klack, now lost.

DESCRIPTION: The breadth is slightly greater than the length, and a centrally placed abactinal swelling is present. The ossicle has a narrow depressed rim covered in fine granule pits, and the central area bears low rugosities conjoined by struts.

REMARKS: The affinities of this form were discussed by Gale (1987a), who considered that its closest relative was *Metopaster hunteri* (Forbes, 1848) from the Coniacian–Campanian chalk of the Anglo-Paris Basin.

Weitschataster Neumann and Girod, 2018

DIAGNOSIS: A small goniasterid with a pentagonal to subpentagonal outline, in which three superomarginals are present on each side of the arm. The marginals are characterised by the presence of rugosities on the surface of the inner border, and rounded granule pits on the lateral part of the border.

TYPE SPECIES: *Weitschataster intermedius* Neumann and Girod, 2018, by original designation.

INCLUDED SPECIES: *Metopaster decipiens* Spencer, 1913, *M. undulatus* Spencer, 1913 and *M. tamarae* Gale, 1987a.

REMARKS: *Weitschataster* is a small goniasterid which possesses distinctively sculptured marginals, typically including both rugosities and rounded granule pits (Neumann and Girod 2018). *Weitschataster undulatus* and *W. decipiens* are common and widespread species in basinal Campanian and lower Maastrichtian chalks (Jagt 2000; Neumann *et al.* 2023) of Germany, Belgium, the Netherlands and the UK.

Weitschataster tamarae (Gale, 1987a)
(Pl. 6, Figs 3–6, 9–11)

1987a. *Metopaster tamarae* Gale, p. 36, pl. 8, figs 6–11.

DIAGNOSIS: *Weitschataster* in which the inferomarginals lack rugosities and possess raised central areas surrounded by regions with fine granule pits.

TYPE: The ultimate superomarginal figured by Gale (1987a, pl. 8, fig. 6) is the holotype (NHMUK PI EE 54238). The other figured ossicles are paratypes (NHMUK PI EE 54239–54243). All are from the upper lower Campanian of Ivö Klack, southern Sweden.

MATERIAL: Over 100 marginal ossicles from the upper lower Campanian of Ivö Klack, southern Sweden.

REMARKS: *Metopaster tamarae* is transferred to the genus *Weitschataster* on account of the close similarities of the sculpture of the superomarginals with those of the type species, *W. intermedius*; the raised central area, bearing rounded granule pits, passes on the inner border into a region of discrete rugosities (compare Text-fig. 8I with Neumann and Girod 2018, fig. 2). However, *W. tamarae* differs in the absence of rugosities on the inferomarginals (Pl. 6, Figs 4, 6) in which the central area becomes broken up towards the borders of the marginals, passing into a marginal zone of very fine spine pits. Additionally, in the reconstruction of Gale (1987a, text-fig. 10.2), *W. tamarae* has three superomarginals on each side of the arm, as in *Weitschataster.* The pedicellariae present on the marginals of *W. tamarae* (Pl. 6, Fig. 4, bottom left-hand part of ossicle) are similar to those in *W. intermedius* (Neumann and Girod 2018, fig. 2f), comprising an oval, central attachment site and narrow lateral depressions to accommodate the valves. The pedicellariae on the actinal ossices of *W. intermedius* (Neumann and Girod 2018, fig. 2e), in contrast, are elongated and have low valves.

Rugametopaster gen. nov.

DIAGNOSIS: Marginals low, lacking raised central areas, and covered with coarse rugosities which become finer towards plate margins. Ultimate inferomarginal is large, triangular and corresponds with a broad surface on the enlarged ultimate superomarginal. Pedicellariae absent.

TYPE SPECIES: *Metopaster rugissimus* Gale, 1987a.

REMARKS: The genus is common in the Kristianstad Basin (southern Sweden), where the type species is present in the Santonian to lower Campanian. An undescribed species, listed as *Metopaster* (?) sp. indet. by Neumann *et al.* (2023, fig. 15A–H) and from the lower Campanian *lingua/quadrata* Zone of Höver, northern Germany, looks similar to *Rugametopaster* gen. nov., but differs from *R. rugissimus* in the coarser, more widely spaced rugosities which are linked by fine radial struts. In addition, the ultimate superomarginal corresponded to three inferomarginals, not one (Neumann *et al.* 2023, fig. 15b).

Rugametopaster rugissimus (Gale, 1987a)
(Pl. 6, Figs 7, 8, 12–16)

1987a. *Metopaster rugissimus* Gale, p. 34, pl. 7, figs 1–5.

DIAGNOSIS: As for genus.

TYPES: The ultimate superomarginal figured by Gale (1987a, pl. 7, fig. 19) is the holotype (NHMUK PI EE 54228). The other figured ossicles are paratypes (NHMUK PI EE 54229–54236).

MATERIAL: Over 200 marginal ossicles from Ivö Klack.

REMARKS: This species was described in detail by Gale (1987a). It is abundant at Ivö Klack.

Haccourtaster Jagt, 2000

DIAGNOSIS: A small, pentagonal goniasterid in which four superomarginals and inferomarginals are typically present on each side of the disc. Blunt internal intramarginal cavities are present between the marginals.

TYPE SPECIES: *Haccourtaster aemstelensis* Jagt, 2000, by original designation.

OTHER INCLUDED SPECIES: *Haccourtaster hrbac* Žítt, 2005b, *Haccourtaster berryensis* Gale and Jagt, 2025, *Haccourtaster liticola* Gale and Jagt, 2025 and *Haccourtaster nattestadae* Gale and Jagt, 2025.

REMARKS: *Haccourtaster* is a distinctive small goniasterid, which typically occurs in marginal marine Upper Cretaceous facies. Although four superomarginals and four inferomarginals are typically present on each side of the disc, a small, distal inferomarginal is found on some specimens. The internal intramarginal cavities (Žítt 2005b, fig. 11A) represent short, narrow extensions of the coelom into the marginal frame and are of unknown function. Species are characterised by distinctive marginal morphologies and external sculptures. *Haccourtaster* probably evolved from a species of *Metopaster*, by retaining four marginals on each side of the disc, either developing paedomorphically from a species with more marginals, or from an ancestor which also possessed four marginals (Gale and Jagt 2025). It developed the distinctive intramarginal cavities in the interior of the marginals, and the ultimate inferomarginal became enlarged to correspond with the ultimate superomarginal.

Haccourtaster liticola Gale and Jagt, 2025
(Pl. 6, Figs 17–22)

2025. *Haccourtaster liticola* Gale and Jagt, 2025, p. 4, fig. 1A–F.

DIAGNOSIS: A relatively large *Haccourtaster* (R = 10–12 mm; r = 8–10 mm) in which the surfaces of the marginals are evenly convex and bear densely and evenly spaced, impressed granule pits and oval pedicellariae.

TYPES: The median superomarginal (Pl. 6, Fig. 19) is the holotype (NHMUK PI EE 18204); the other figured marginals are paratypes (NHMUK PI EE 18200–18223), all from the upper lower Campanian of Ivö Klack.

MATERIAL: Over 100 isolated marginals ossicles from the type locality and horizon (NHMUK, A.S. Gale Collection).

REMARKS: *Haccourtaster liticola* differs from all other species of the genus in its evenly tumid marginals which possess dense, evenly spaced granule pits of equal dimensions (Gale and Jagt 2025).

Ivoaster gen. nov.

DIAGNOSIS: A goniasterid in which the marginals are nearly cuboid, and in which the inner actinal and abactinal surfaces are truncated and slope internally. The lateral surface of the superomarginals carry one or two, variably slanted, slit-like pedicellariae.

TYPE SPECIES: *Ivoaster soerensenae* sp. nov.

DERIVATION OF NAME: After Ivö Klack.

REMARKS: Distinctive marginal ossicles from Ivö Klack evidently belong to the Goniasteridae as the superomarginals possess slit-like valvate pedicellariae restricted to this family, and are characteristic of Cretaceous genera such as *Ophryaster* Spencer, 1913 and *Tomidaster* Sladen, 1891. However, they are most unusual in that the actinal and abactinal surfaces of the marginals are truncated and slope at an angle of approximately 45º to the intermarginal contact. These surfaces articulated with exceptionally thick abactinal and actinal ossicles, and the body cavity was therefore very thin. Truncated inferomarginals like these are found in some oreasterids such as *Protoreaster* Döderlein, 1916, but the superomarginals in this genus are tall, and slit-like pedicellariae are not found in oreasterids. The outline of the taxon was pentagonal, and the arms short.

Ivoaster soerensenae gen. et sp. nov.
(Pl. 7, Figs 9–15)

DIAGNOSIS: As for genus.

TYPES: The superomarginal figured in Pl. 7, Fig. 9 is the holotype (NHMUK PI EE 18375). The other marginal figured (Pl. 7, Figs 10–15) are paratypes (NHMUK PI EE 18376–18383), all are from the upper lower Campanian at Ivö Klack.

MATERIAL: 68 marginal ossicles from the type locality.

DERIVATION OF NAME: For Anne Mehlin Sørensen, in honour of her work on the fauna of Ivö Klack and for help in collecting the type material.

DESCRIPTION: Marginals nearly square in actinal and abactinal views, sub-cuboidal in form (Pl. 7, Figs 9–14), proximal and distal margins parallel. Articulation facets for abactinal and actinal ossicles tall and slanted at nearly 45º to the intermarginal surfaces. Inferomarginals possess more or less discrete actinal and lateral surfaces, superomarginals with single, convex lateral surface (Pl. 7, Fig. 11). Lateral surfaces of superomarginals bear one or two slit-like pedicellariae, variably angled to the intermarginal surface (Pl. 7, Fig. 9, 10, 12). Distal marginals (Pl. 7, Fig. 15) taper towards the arm tip. External surfaces of marginals bear even covering of fine, shallow granule pits.

Pycinasteridae Spencer and Wright, 1966

DIAGNOSIS: Disc broad, interradii nearly straight or gently concave. Marginals of disc tall, upright, forming a palisade-like margin to the disc. Arms narrow, superomarginals meeting over radius or separated by a single row of radials. The first (interradial) pair of supero- and inferomarginals oppose; distally, these alternate. Large papular spaces are present at ambitus between interradial marginals. Pedicellariae large, rounded-pentagonal in outline and bearing 5 valves; only one or two present on each marginal. A single, large, laterally compressed spine present in each actinal interradius (modified from Gale 1988).

INCLUDED GENERA: *Pycinaster* Spencer, 1907 only.

REMARKS: As Blake *et al.* (2015) have pointed out, *Pycinaster* is a poorly known and little-described genus and for this reason, I have assembled images of specimens to illustrate important morphological features (Pl. 7, Fig. 8; Text-fig. 3A–F). A most striking feature of large species is the tall, vertical interradial margin formed by infero- and superomarginals which are short and tall (Pl. 7, Fig. 8; Text-fig. 3E, F, G); the median superomarginals taper actinally towards the ambitus. The abactinal margin of the superomarginals is domed (Pl. 7, Fig. 8; Text-fig. 3A) and the interradial supero-and inferomarginals oppose (Pl. 7, Fig. 8). Distally, supero-and inferomarginals alternate and decrease rapidly in height. There are large spaces between the interradial marginals close to the ambitus which were occupied by papulae (Pl. 7, Fig. 8; Text-fig. 3F). The actinal interareas each bear a large, laterally compressed, downwardly directed spine (Text-fig. 3B, C) set halfway between the peristome and the margin. These can be separated in sets of associated marginals (Text-fig. 3H) and are nearly equal in length to the height of the interradial marginals. The pedicellariae (Text-fig. 3G) are set in depressions, have a rounded-pentagonal outline and five valves. There are usually only one or two pedicellariae on each marginal.

The affinities and phylogenetic position of the extinct (Jurassic–Miocene) Pycinasteridae are not clear. *Phocidaster* Spencer, 1913, type species *P. grandis* Spencer, 1913, refers simply to large interradial superomarginals of a *Pycinaster* (Gale 1988) and the former genus is therefore placed in synonymy with the latter.

Pycinaster Spencer, 1907

DIAGNOSIS: As for family.

TYPE SPECIES: *Goniaster* (*Goniodiscus*) *angustatus* Forbes, 1848, by original designation.

INCLUDED SPECIES: *Pentagonaster robustus* Sladen, 1891, *Oreaster obtusus* Forbes, 1848, *Pycinaster crassus* Spencer, 1907, *Pycinaster magnificus* Spencer, 1913, *Pycinaster humilis* Spencer, 1913, *Phocidaster grandis* Spencer, 1913, *Pycinaster danicus* Nielsen, 1943, *Pycinaster cornutus* Rasmussen, 1945, *Pycinaster rasmusseni* A.H. Müller, 1953 and *Pycinaster christenseni* sp. nov.

REMARKS: Most of the species listed above are only known from isolated marginals. The superbly preserved material from the chalk of the UK (Sladen and Spencer 1890–1907) and northern Germany (Schulz and Weitschat 1971; Neumann *et al.* 2023) needs taxonomic revision.

Pycinaster christenseni sp. nov.
(Pl. 7, Figs 1–7)

DIAGNOSIS: *Pycinaster* in which the marginals bear a narrow, depressed border, and fine, shallow, evenly distributed spine pits.

TYPE: The interradial superomarginal figured here (Pl. 7, Fig. 1) is the holotype (NHMUK PI EE 18368), and the other figured marginals (Pl. 7, Figs 2–7) are paratypes (NHMUK PI EE 18369–18374). All are from the upper lower Campanian of Ivö Klack.

MATERIAL: 87 marginal ossicles from the type locality.

DERIVATION OF NAME: For the late Walter Kegel Christensen, Copenhagen, in honour of his work on Late Cretaceous belemnites and stratigraphy.

DESCRIPTION: Interradial superomarginals (Pl. 7, Figs 1, 6) tall, symmetrical, height twice maximum breadth, abactinal margin convex, ossicle tapering towards ambitus where there is contact with a single interradial inferomarginal. Distal/proximal surfaces bear a deep concavity (Pl. 7, Fig. 7). Superomarginals from distal part of disc (Pl. 7, Figs 2–4) are slightly asymmetrical, with the distal margin lower than the proximal margin and have a slight abactinal taper. The external surface of all superomarginals has a poorly defined depressed margin, and the central area has a cover of evenly spaced, fine, shallow spine pits which fade towards the ambitus. One to three rounded pedicellariae are present on the lower part of the superomarginals. Inferomarginals (Pl. 7, Fig. 5) with evenly convex lateral margin.

REMARKS: *Pycinaster christenseni* sp. nov. differs from its congeners in having a poorly defined, depressed border on the marginals and a sculpture of very fine, shallow spine pits. The sculpture of *Pycinaster* marginals is highly variable; many specimens are virtually smooth (e.g., Neumann *et al.* 2023, figs 38–40), but an undescribed form from the lower Campanian of the UK (Pl. 7, Fig. 8) possesses rugosities on the ambital portion of the marginals, and fine spine pits on the actinal and abactinal parts of the marginals.

Stauranderasteridae Spencer, 1913

DIAGNOSIS: Disc domed, including enlarged primary interradials and centrale. Supero- and inferomarginals alternate and imbricate proximally in part of the radius.

INCLUDED GENERA: *Aspidaster* de Loriol, 1884, *Hadranderaster* Spencer, 1907, *Stauranderaster* Spencer, 1907, *Stauraster* Valette, 1929 and *Manfredaster* Villier, Breton, Margerie and Néraudeau, 2003.

REMARKS: Stauranderasterids include a heterogeneous assortment of Jurassic–Paleocene asteroids which were abundant and diverse in the Upper Cretaceous. They have received relatively little attention, although Villier *et al.* (2003) performed a cladistic analysis on a number of taxa and concluded that the group was monophyletic and that *Stauranderaster* and *Manfredaster* were the most derived genera. The relationship between stauranderasterids and the similar Paleogene–present day oreasterids has not been resolved.

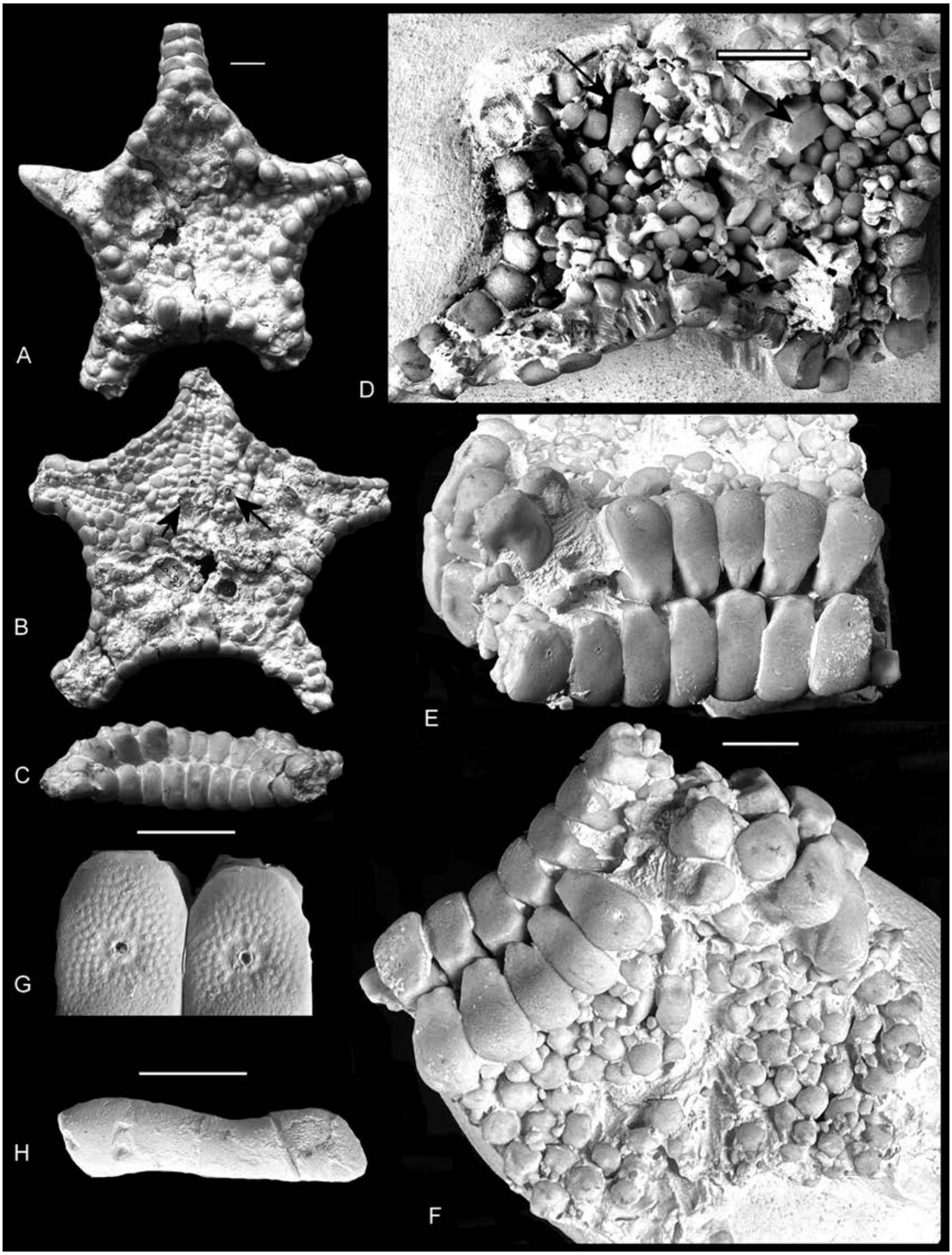
Manfredaster Villier, Breton, Margerie and Néraudeau, 2003

DIAGNOSIS: Disc large, domed, arms short, distally swollen. The distal arm is made up of enlarged radials and tall superomarginals. Pedicellariae with cup-shaped basal piece. Marginals and radials of proximal arm and disc imbricate proximally.

TYPE SPECIES: *Manfredaster cariniferus* Villier, Breton, Margerie and Néraudeau, 2003, by original designation.

INCLUDED SPECIES: *Oreaster bulbiferus* Forbes, 1848, *Aspidaster concinnus* Breton, 1979 and *Manfredaster graveseni* sp. nov.

REMARKS: *Manfredaster* is a distinctive stauranderasterid, in which the domed disc bears enlarged, tumid primary interradials and a centrale; the distal arms are club-like, expanded both laterally and ver-



Text-fig. 3. Representatives of *Pycinaster* Spencer, 1907. A–F – *Pycinaster angustatus* (Forbes, 1848); A–C – near-complete individual, in abactinal, actinal and lateral views, respectively (NHMUK PI EE 20293); D – Actinal surface of partial specimen (BGS 109521); E, F – partial individual in lateral interradial and abactinal views, respectively (BGS 109520). G, H – *Pycinaster magnificus* Spencer, 1913, interradial inferomarginals, to show pedicellariae (NHMUK PI EE 18339) and actinal spine, in lateral view (NHMUK PI EE 18340). Provenance: A–C is from the *Micraster coranguinum* echinoid Zone, upper Coniacian or lower Santonian, Micheldever, Hampshire, UK; E, F is from the *Micraster coranguinum* echinoid Zone, upper Coniacian or lower Santonian, Gravesend, Kent, UK; G is from the *Offaster pilula* echinoid Zone, lower Campanian, East Harnham, Salisbury, Wiltshire, UK; H is from the *Belemnitella mucronata* belemnite Zone, upper Campanian, Alum Bay, Isle of Wight, UK. Arrows in B and D indicate large actinal spines. Scale bars equal 10 mm (A–C), 5 mm (D–F) and 3 mm (G).

tically (Pl. 8, Fig. 1). The distal arms are comprised of tall superomarginals and usually, large, abactinally swollen radial ossicles (Pl. 8, Figs 2, 3). The proximal marginals and radials are wedge-shaped and imbricate strongly towards the centre of the disc. Pedicellariae have a cup-shaped basal piece. Niebuhr and Seibertz (2016) described *Manfredaster praebulbiferus* from the upper Cenomanian of Dresden-Plauen, eastern Germany, based on isolated ossicles. However, their material comprises a mixture of superomarginals of the goniasterid *Metopaster* and diverse ossicles of *Manfredaster*; the designated holotype is a median superomarginal of *Metopaster* sp. (Niebuhr and Seibertz 2016, fig. 4d; MMG SaK 15803). Their reconstruction (Niebuhr and Seibertz 2016, fig. 5) is a chimaera based on a mixture of goniasterid marginals and diverse stauranderasterid ossicles.

Manfredaster graveseni sp. nov.
(Pl. 8, Figs 4–14)

DIAGNOSIS: A small *Manfredaster,* in which the primary interradials are oval and only slightly domed. All abactinals and marginals possess a sharply defined central area which bears large, round, evenly spaced granule pits.

TYPE: A primary interradial from the madreporic interradius (Pl. 8, Fig. 8) is the holotype (NHMUK PI EE 18311). The other figured ossicles are paratypes (NHMUK PI EE 18312–18324), all from the upper lower Campanian at Ivö Klack.

MATERIAL: 78 ossicles, including marginals, abactinal ossicles and radials from the type locality.

DERIVATION OF NAME: For the late Palle Gravesen, Copenhagen, exceptional fossil collector and scientist.

DESCRIPTION: Abactinal primary interradial ossicles (Pl. 8, Figs 7, 9) convex, suboval to crescentic in outline; those from the madreporic interradius (Pl. 8, Fig. 8) are subrectangular with a concave distal surface which articulates with the madreporite. Marginals from the distal disc and proximal arms (Pl. 8, Figs 10, 14) were imbricated with the outer surface convex, arched. Superomarginals from the swollen distal arm (Pl. 8, Figs 6, 11, 12) have a tall internal contact with the radials, a gently convex exterior surface and a broad contact with the inferomarginals. Distal inferomarginals (Pl. 8, Fig. 5) are low and distal radials (Pl. 8, Fig. 6, middle ossicle) tall, tapering actinally, with a convex abactinal margin. All ossicles possess a sharply delimited, slightly raised central area which bears rather coarse, evenly spaced spine pits.

REMARKS: *Manfredaster graveseni* sp. nov. appears most closely allied to *M. concinnus* from the Santonian of Normandy, France (Breton 1979, pl. 1) in the relatively weakly expanded distal arms. However, in *M. concinnus* the distal inferomarginals appear to be taller than the superomarginals and the external face of the marginals lacks a central area and has fine, shallow granule pits.

Podosphaerasteridae Fujita and Rowe, 2002

DIAGNOSIS: Body spherical to subspherical, ambulacral grooves extending up to ambitus. Body wall made up of few, fairly large equidimensional ossicles which are not differentiated into abactinals, marginals and actinals. Body wall adjacent to peristome made up of two inset chevrons of large, straight-sided ossicles and single unpaired actinal plate. An additional row of plates are intercalated between the primary interradials and primary radials. Four radial ossicles only present distal to the primary radials. Ambulacrals short, rectangular. Adambulacrals possessing rugose actinal faces. Oral ossicles with large oval body, and short, Y-shaped apophyse (Gale 2021).

INCLUDED GENERA: *Valettaster* Lambert, 1914, *Podosphaeraster* Clark and Wright, 1962, *Rugosphaeraster* Gale, 2021 and *Vectisaster* gen. nov.

Valettaster Lambert, 1914

DIAGNOSIS: Podosphaerasterid in which undifferentiated primary body ossicles look like truncated cones, their flat tops forming external face of ossicle, carrying beads of imperforate stereom. Interstices between faces of abactinal ossicles packed with smaller ossicles, also carrying beaded sculpture. Together, primaries and interstitial ossicles form flush outer surface. Tiny papular pores formed by embayments in two or three interstitial ossicles (Gale 2021).

TYPE SPECIES: *Oreaster ocellatus* Forbes, 1848, by subsequent designation Rasmussen (1950).

INCLUDED SPECIES: *Sphaerites digitatus* Quenstedt, 1858, *Stauranderaster argus* Spencer, 1907, *Valettaster granulatus* Nielsen, 1943, *Valettaster stipes* Villier, 2010 and *Valettaster thuyi* Gale, 2021.

REMARKS: *Valettaster* is a long-ranging genus, extending from the Lower Jurassic (Pliensbachian) to the Paleocene (Danian). It is distinguished by the distinctive primary ossicles which have the form of truncated cones bearing a flat external surface.

Valettaster argus (Spencer, 1907)
(Pl. 5, Figs 17, 18)

1850. fragment of an *Oreaster* Forbes in Dixon, pl. 21, fig. 16.
1907. *Stauranderaster argus* Spencer, p. 99, pl. 29, fig. 8.
1913. *Tholaster argus* (Spencer); Spencer, p. 138, pl. 13, fig. 25.
1914. *Valettaster ocellatus* (Forbes); Valette, p. 60, fig. 20.
1985. *Valettaster argus* (Spencer); Breton, p. 91, fig. 6.
2021. *Valettaster argus* (Spencer); Gale, p. 43, figs 6H–K, N, O, 7P, R, 8K, M, 22L, 23B–P.

DIAGNOSIS: *Valettaster* in which the abactinal ossicles possess small external faces with a reticulate sculpture.

TYPE: The individual from the Santonian *Marsupites* crinoid Zone of Brighton, southern England (NHMUK PI EE 5109), is the holotype.

MATERIAL: Two primary ossicles from Ivö Klack (NHMUK PI EE 18325, 18326).

REMARKS: The two ossicles (Pl. 5, Figs 17, 18) are referred to this species on account of the relatively small external face which forms the summit of the truncated cone on one specimen (Pl. 5, Fig. 18; compare with Gale 2021, fig. 23H). The other specimen (Pl. 5, Fig. 17) lacks an external face entirely, as do some ossicles of *Valettaster argus* (Gale 2021, fig. 23H, left-hand side).

Rugosphaeraster Gale, 2021

DIAGNOSIS: Body domed, actinal surface flat. Robust abactinal ossicles irregularly polygonal to rhombic, mostly equidimensional, with notches for papulae at corners. Surface of abactinal ossicles bearing transverse strips or irregularly radial pustules of imperforate stereom (Gale 2021).

TYPE SPECIES: *Rugosphaeraster ruegenensis* Gale, 2021, by original designation.

REMARKS: The genus is highly distinctive, on account of the ridged and pustulate abactinal ossicles. The single articulated specimen known to date (Pl. 9, Figs 14–16) shows body form to be domed, with a flat base. No ossicles other than abactinals known. Exact affinities of the genus are obscure, but the general body shape and large abactinals suggest a place within the Podosphaerasteridae.

Rugosphaeraster ruegenensis Gale, 2021
(Pl. 9, Figs 14–17)

2021. *Rugosphaeraster ruegenensis* Gale, p. 47, fig. 26A–Q.
2023. *Rugosphaeraster* cf. *ruegenensis* Gale; Neumann *et al*., p. 510, fig. 42D–F.

DIAGNOSIS: As for genus.

TYPE: The associated and partly articulated ossicles originating in an individual, figured by Gale (2021, fig. 26A) are the holotype (SNSB-BGSP 2020 XLV4).

MATERIAL: One actinal/abactinal ossicles from Ivö Klack (NHMUK PI EE 17698).

REMARKS: The single ossicle (Pl. 9, Fig. 17) is confidently assigned to this species by comparison with those of the exceptionally preserved entire specimen (Pl. 9, Figs 14–16) from the lower Campanian of the Hannover area, northern Germany. The strongly ridged exterior, notches for papulae and lateral articular surfaces are identical to those on material from Rügen figured by Gale (2021, fig. 26).

Vectisaster gen. nov.

DIAGNOSIS: Presumed abactinal ossicles rounded to hexagonal, with raised central region comprising strips of imperforate stereom arranged radially, in anastomosing parallel groups, or in V-shaped arrays.

TYPE SPECIES: *Vectisaster enigmaticus* gen. et sp. nov.

REMARKS: Small, very distinctive ossicles are present in both basinal chalks of late early Campanian age at Whitecliff, Isle of Wight, UK and at Ivö Klack, Sweden. Although the external sculpture of strips of imperforate stereom resembles that of *Rugosphaeraster* (Pl. 9, Figs 15, 17), the margins of the ossicles are thin and lack specialised articulation structures or gaps for extrusion of papulae that are present in *Rugosphaeraster* (Pl. 9, Fig. 17; Gale 2021, fig. 26A–N). The genus is placed in the Podosphaerasteridae with considerable uncertainty.

Vectisaster enigmaticus gen. et sp. nov.
(Pl. 9, Figs 1–8, 11–13)

DIAGNOSIS: As for genus.

TYPES: The primary ossicle, probably an abactinal, figured in Pl. 9, Fig. 1 is the holotype (NHMUK PI EE 18327). The other figured ossicles (Pl. 9, Figs 2–8, 11–13) are paratypes (NHMUK PI EE 18328–18238). The holotype, and five paratypes (Pl. 9, Figs 1–6), are from the upper Culver Chalk Formation, *Gonioteuthis quadrata* belemnite Zone (lower Campanian) of Whitecliff, Isle of Wight, UK. The other paratypes (Pl. 9, Figs 7, 8, 11–13) are from the upper lower Campanian at Ivö Klack, southern Sweden.

MATERIAL: Twenty-five additional ossicles from Whitecliff and Ivö Klack (NHMUK, A.S. Gale Collection).

DESCRIPTION: Ossicles hexagonal to oval in outline, approximately equidimensional, flattened internally, convex externally. A raised central area comprises strips of imperforate stereom which are arranged either in a V-shaped array (Pl. 9, Fig. 1) or form vertical, impersistent, anastomosing strips (Pl. 9, Figs 2–4, 7, 8, 12, 13). A flat region constructed of fine stereom forms one side of the external face. Ossicles which are presumed to be more abactinal in position (Pl. 9, Fig. 6) are low and have ridges radiating outwards and downwards, resembling madreporites; there are also ossicles which are transitional between both types (Pl. 9, Figs 5, 11). Contacts between the ossicles are low and do not have articular structures or notches for papulae.

Podosphaerasteridae or Sphaerasteridae, affinities uncertain
(Pl. 5, Fig. 16, Pl. 9, Figs 9, 10)

MATERIAL: A single flat, hexagonal ossicle (Pl. 9, Figs 9, 10) and an adambulacral ossicle (Pl. 5, Fig. 16).

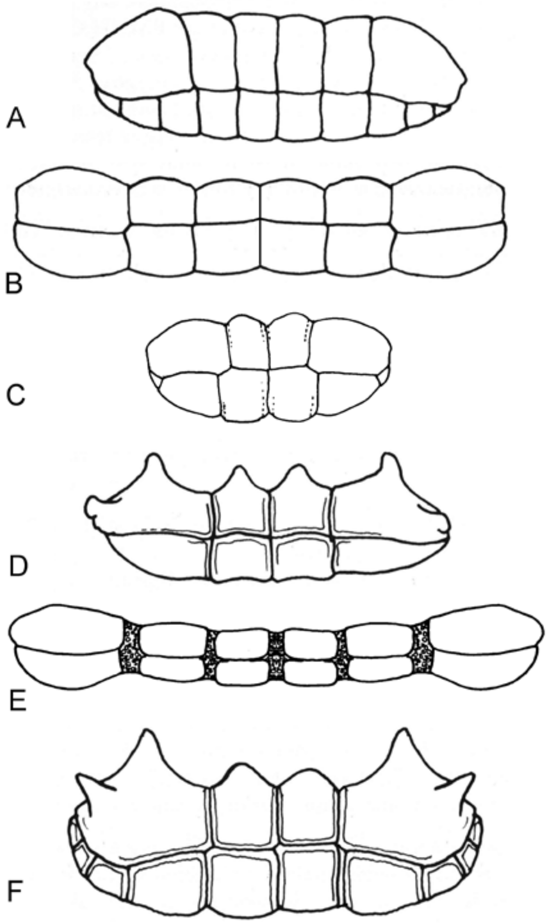
DESCRIPTION: The abactinal/actinal ossicle (Pl. 9, Figs 9, 10) is hexagonal, flattened and a narrow, depressed rim is present. The external surface has irregularly arranged, anastomosing strips of stereom. The regularly polygonal shape is similar to that of ossicles of various sphaerasterids, such as *Eosphaeraster* Gale, 2021, but the margin lacks articular facets and papular gaps found on all sphaerasterids and podosphaerasterids (Gale 2021). The adambulacral (Pl. 5, Fig. 16) is tall, swollen actinally and has a vertically oriented ligament pit in place of an interadambulacral muscle, a characteristic of sphaerasterids and podosphaerasterids (Gale 2021); it could possibly belong to *Valettaster*.

MODES OF LIFE OF IVÖ KLACK ASTEROIDS

Shallow-water asteroids have diverse modes of life, which vary greatly between families, genera and species (Lawrence 2013). In the palaeoenvironments represented by the Ivö Klack succession, there presumably was a fundamental difference between taxa living on the hard substrates provided by gneiss boulders and those found in the intervening carbonate sand and shell gravels. Interpreting mode of life can be achieved in part by comparisons of taxa found at Ivö Klack with their nearest living relatives. Thus, astropectinids (represented at Ivö Klack by three species) are all specialist shallow-burrowing taxa, predating on infauna, most notably bivalve molluscs (Jangoux 1982; Ventura 2013). In contrast, many asterinids (one species at Ivö Klack) live on hard substrates in the lower intertidal and subtidal, and feed by browsing on epizoans and surface films using stomach eversion (Clark and Downey 1992, p. 171).

There is a single pterasterid at Ivö Klack; the shallow-water (10–100 m), northeast Pacific pterasterid *Pteraster tesselatus* lives on hard substrates in high-energy environments and feeds on sponges and ascidians by stomach eversion (Lambert 2000). Pterasterids are protected by producing copious quantities of mucus (Nance and Braithwaite 1981). Asteriids (two species at Ivö Klack) are epifaunal predators, primarily on bivalve molluscs, and the small Ivö Klack species can perhaps be compared with the living genus *Coscinasterias* (Barker 2013) in New Zealand. *Coscinasterias* lives in and under rocks, and is a voracious predator on molluscs, which are eaten by stomach eversion.

Identifying the life habits of the diverse assemblage of goniasterids found at Ivö Klack (nine species) is more difficult. Many present-day, shallow-water goniasterids can live on both hard and soft substrates, such as *Mediaster aequalis* Stimpson, 1857, in the northeast Pacific (Lambert 2000). This species has very diverse feeding habits. On rocky substrates, it feeds by stomach eversion on sponges and ectoprocts, whereas on sandy bottoms it ingests pennatulids, while deposit feeding on muddy substrata (Mauzey *et al.* 1968). However, the predominantly southwest Pacific-Indian Ocean genera *Tosia* Gray, 1840 and



Text-fig. 4. Lateral views of margins in fossil (A–D, F) and extant (E) goniasterids. A – *Metopaster elegans* Gale, 1987a;. B – *Rugametopaster rugissimus* (Gale, 1987a); C – *Haccourtaster liticola* Gale and Jagt, 2025; D – *Metopaster calcar* Spencer, 1913; E – *Pentagonaster pulchellus* Gray, 1840; F – *Metopaster bromleyi* Gale, 1987a.

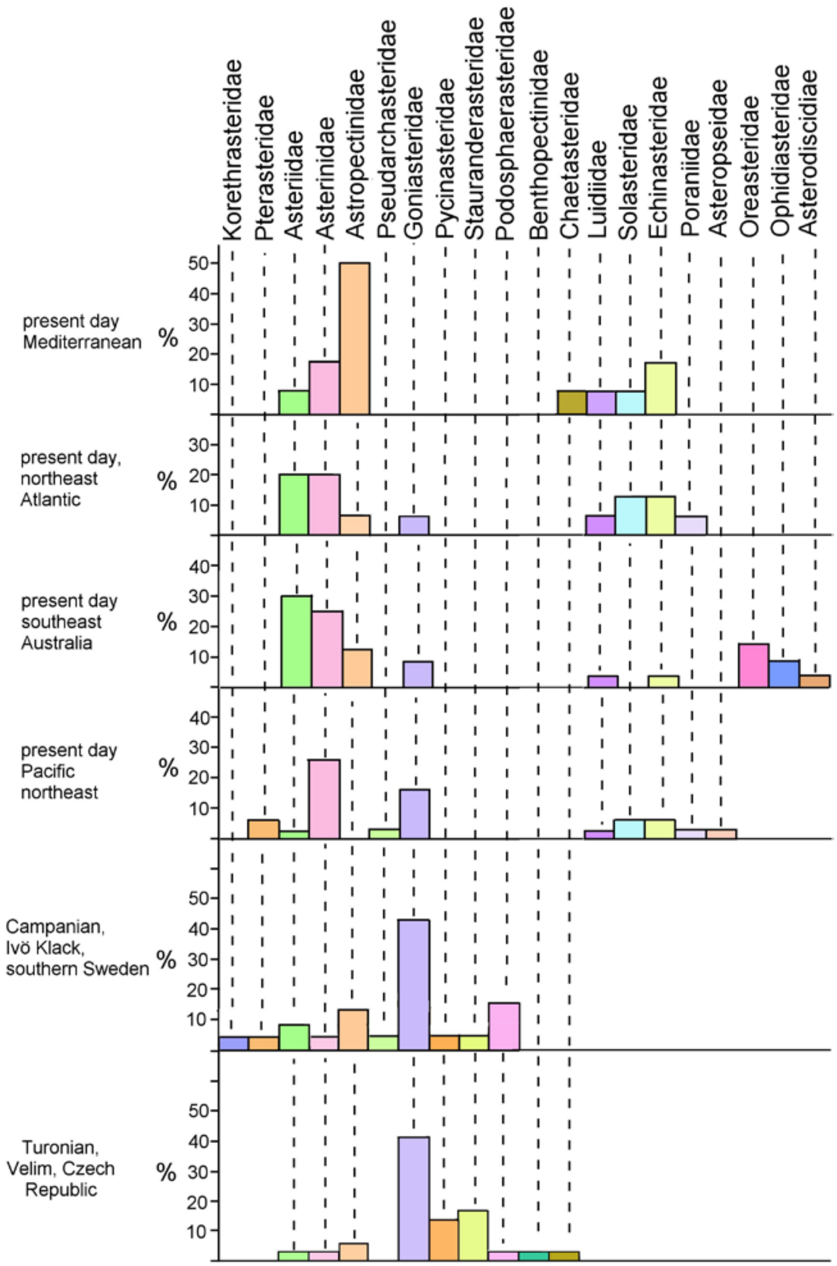
Pentagonaster Gray, 1840 live on rocky substrata in shallow waters and feed by stomach eversion on epifauna and algae. *Pentagonaster*, in particular, has a number of morphological features which invite comparison with certain goniasterid species from Ivö Klack. In *Pentagonaster pulchellus* Gray, 1840, a single, large distal inferomarginal contacts the enlarged ultimate superomarginal (Text-fig. 4E), precisely as in the Ivö Klack species *Metopaster calcar* and *Rugametopaster rugissimus* (Text-fig. 4B, D). This is perhaps an adaptation, strengthening the distal arm in high-energy, exposed habitats. A dense cover of granular spines on both the actinal and abactinal surfaces in goniasterids appears to be an adaptation to living on fine, soft substrates; species in which the marginal ossicles lack these, such as *Metopaster calcar* and *Rugametopaster rugissimus* were more likely to be hard substrate specialists. The spike-like processes on both the superomarginals of both *Metopaster calcar* and *M. bromleyi* (Text-fig. 4) were likely to have been deterrents to predation.

The Pycinasteridae and Stauranderasteridae (both with one species at Ivö Klack) are extinct, but species with very similar morphology lived predominantly on the soft substrata in basinal chalks of equivalent age (early Campanian) to the Ivö Klack rocky coast. It is therefore most probable that these also lived on soft substrates there. The life habits of extant podosphaerasterids are poorly known (Gale 2021), although they are possibly spongivores.

COMPARISON WITH ROCKY SHORE ASTEROID ASSEMBLAGES FROM THE LOWER TURONIAN OF THE CZECH REPUBLIC

Asteroid ossicles are common in deposits formed on rocky shores of late Cenomanian–early Turonian age on the margins of the Bohemian Cretaceous Basin in the Czech Republic (Žítt *et al.* 1997; Žítt 2004). Many occur in the infill of deep channels cut into the Proterozoic basement rocks. Žítt (2005a, b) provided detailed descriptions of two taxa, and a general account of the asteroid faunas (Žítt 2004). Further information on the asteroids was obtained from a collection of ossicles from the lower Turonian of Velim (Czech Republic) sent to me by Tomaš Kočí (Prague).

Žítt (2004) recorded 29 species from the nearshore upper Cenomanian–middle Turonian interval of the Bohemian Cretaceous Basin, including 13 goniasterids, five stauranderasterids, four pycinasterids, two astropectinids and one species each of sphaerasterid, benthopectinid, asteroid and chaetasterid (note that *Arthraster* Forbes, 1848 is a chaetasterid; Gale 2020b). The material from Velim includes an additional species of asterinid (*Scaniasterina* gen. et sp. nov.; see above). The percentages of taxa of each family are shown in Text-fig. 5. The asteroid fauna is dominated by diverse goniasterids (43%) which are also very abundant. This is closely similar to the Ivö Klack goniasterid diversity (42%), and some taxa from both regions are closely related (*Nymphaster* spp., *Haccourtaster* spp.). *Metopaster bromleyi* from Ivö Klack is a likely descendant of the Turonian *Metopaster thoracifer* (see above, and Gale and Jagt 2025). Stauranderasterids and pycin-



Text-fig. 5. Composition of asteroid fauna from Ivö Klack in comparison to present-day faunas from shallow-marine habitats at the present day. Data from P. Lambert (2000, northeast Pacific), Koehler (1924, Mediterranean), Australian Museum, accessed at https://Australian.museum>learn>animals>seastars-starfish (southeast Australia); Clark and Downey (1992, northeast Atlantic) and Žítt (2004, Bohemian Cretaceous Basin, Czech Republic).

asterids are present in both assemblages, but more diverse in the Bohemian Cretaceous Basin faunas (17% and 14%, respectively), as compared to 4% for each at Ivö Klack. There is a single sphaerasterid species in the Bohemian Cretaceous Basin (3%) as compared to four at Ivö Klack (15%). The asterinid genus *Scaniasterina* gen. nov. is represented by a single species at each locality. Chaetasterids and benthopectinids are absent from the Ivö Klack assemblages, but present as rarities in the Bohemian Cretaceous Basin.

In terms of overall comparison, the Ivö Klack and

Bohemian Cretaceous Basin asteroid faunas are very similar in generic composition, but the species are all different, as might be expected with an age difference of about 13 myr and geographical separation of 700 km. However, the two Cretaceous faunas differ very significantly from present-day, shallow-marine asteroid faunas (see below).

ROCKY COAST *VS.* BASINAL CHALK ASTEROID ASSEMBLAGES

A remarkable feature of the Ivö Klack asteroid assemblage is that five (20%) of the taxa represented are identical, or very closely related, to species which lived in the contemporaneous, much deeper water (100–300 m), soft- bottomed basinal chalk environments (*Pteraster* cf. *cretachiton*, *Lophidiaster pygmaeus*, *Valettaster argus*, *Rugosphaeraster ruegenensis* and *Vectisaster enigmaticus* gen. et sp. nov.). These must have been very tolerant of diverse substrates and energy levels. Additionally, 16 (64%) of the species belong to genera which are typical of and widely occurring in basinal chalks over much of the Upper Cretaceous. It therefore likely that the endemic shallow-water Ivö Klack species originally evolved from deeper water taxa.

COMPARISON WITH ASTEROID ASSEMBLAGES FROM THE CAMPANIAN OF FRANCE

Villier *et al.* (1997) analysed French asteroid assemblages from diverse Campanian facies of contrasting water depths, in a study extending from calcarenitic chalks of Haute Normandie (NW France), through biocalastic to nearshore marls and sands in Poiteau-Charentes (SW France) and sandy marls and chalks in Occitanie (SE France). They divided the asteroid assemblages into “type *Metopaster*”, “type *Nymphaster*”, “type *Craterast*er”, “type Stauranderasteridae” and “type Astropectinidae” and plotted these groups against depth:facies cross-sections (Villier *et al.* 1997, fig. 3). What is remarkable is the persistent presence of each of these groups in diverse facies representing contrasting palaeoenvironments deposited in different water depths. Although the “type *Craterast*er” group is absent at Ivö Klack, and the “type *Metopaster*” is highly diverse there, the overall composition of the coastline asteroid fauna is broadly similar at the generic level to assemblages present in deeper water facies.

COMPARISON WITH EXTANT SHALLOW-WATER ASTEROID FAUNAS

The occurrence of asteroid families from geographically widespread, present-day shallow-water (<30 m) environments is plotted in Text-fig. 5 for comparison with the Ivö Klack and Bohemian Cretaceous Basin faunas. The available data do not distinguish between taxa from different substrates, but both rocky and soft substrates are present in all regions. A major difference between Cretaceous and present-day, shallow-marine asteroid faunas is the high diversity of goniasterids in Cretaceous deposits (>40%) as compared with the present day (0–16%). Stauranderasterids and pycinasterids occur commonly in Cretaceous deposits but are now extinct. Sphaerasterids are absent from shallow-marine, extant asteroid assemblages.

A further significant difference between the Cretaceous and the present day is in the nearly ubiquitous presence of luidiids, solasterids, echinasterids and poraniids in most modern regions investigated, and the complete absence of these families from Ivö Klack and the Bohemian Cretaceous Basin. It is possible that some of these families, diverse at the present day, had not undergone radiation, or even appeared, by the Late Cretaceous. Luidiids are first known from the Miocene, and echinasterids have no fossil record (Gale 2011). Mesozoic solasterids are only known from a single specimen from the Middle Jurassic (Gale and Ward 2024), and poraniids from a single Middle Jurassic species (Hess 1972). Asterinids are very rare in the fossil record (Gale 2011), being mostly represented by tremasterines from the Jurassic (Gale 2018). The occurrence of *Scaniasterina* gen. nov. in the Upper Cretaceous is the oldest record of an asterinid in shallow water deposits; at the present day they are diverse in rocky shoreline settings (Text-fig. 5). Ophidiasterids, oreasterids and asterodiscids are warm-water groups only present in southern Australia within the regions studied and are absent from the Cretaceous.

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PLATE 1

1 – *Pteraster pulvillus* Sladen, 1889, ambulacral ossicle, in abactinal view.

2, **3**, **11**, **12**, **15** – *Pteraster* cf. *cretachiton* Gale, 2022a. 2, 3 – ambulacral ossicles, in abactinal and actinal views, respectively; the original of Gale (2022a, fig. 8A) (NHMUK PI EE 17744, 18341); 11, 12 – abactinal ossicles, the originals of Gale (2022a, fig. 8H, I) (NHMUK PI EE 17745, 17746); 15 – adambulacral, in actinal view, the original of Gale (2022a, fig. 8K) (NHMUK PI EE 17747).

4, **10**, **17**, **19** – *Remaster gourdoni* Koehler, 1912. 4 – actinal view of adambulacral; 10 – abactinal ossicles bearing fascicles of spines; 17 – primary interrradial ossicle, actinal view; 19 – oral ossicle in interradial view.

5 – *Peribolaster lictor* Fell, 1958, actinal view of adambulacral.

6, **7**–**10**, **16**, **18** – *Remaster cretaceus* sp. nov. 6 – actinal view of broken adambulacral (paratype), the original of Gale (2022a, fig. 8D) (NHMUK PI EE 17739); 7–10 – abactinal ossicles in abactinal view (paratypes); 9, 10 – the originals of Gale (2022a, fig. 8F, G) (NHMUK PI EE 17740, 17741); 16 – primary interadial ossicle, in actinal view, the original of Gale (2022a, fig. 8J) (NHMUK PI EE 17743); 18 – oral ossicle (holotype), in interradial view, the original of Gale (2022a, fig. 8C) (NHMUK PI EE 17738).

14 – *Pteraster cretachiton* Gale, 2022a, adambulacral, in actinal view (NHMUK PI EE 18258).

20 – *Peribolaster biserialis* Fisher, 1910, oral ossicle in radial view.

Figure 1 is from the present day of the North Atlantic. Figures 2, 3, 6, 7–9, 11, 12, 15, 16, 18 are from the upper lower Campanian at Ivö Klack, southern Sweden. Figures 4, 10, 17, 19 are from the present day of the Falkland Islands, South Atlantic. Figure 5 is from the present day of New Zealand. Figures 13, 20 are from the present day of Alaska, northeast Pacific. Figure 14 is from the lower Campanian, *Gonioteuthis quadrata* belemnite Zone at Mottisfont, Hampshire, UK.

Scale bars equal 0.5 mm.

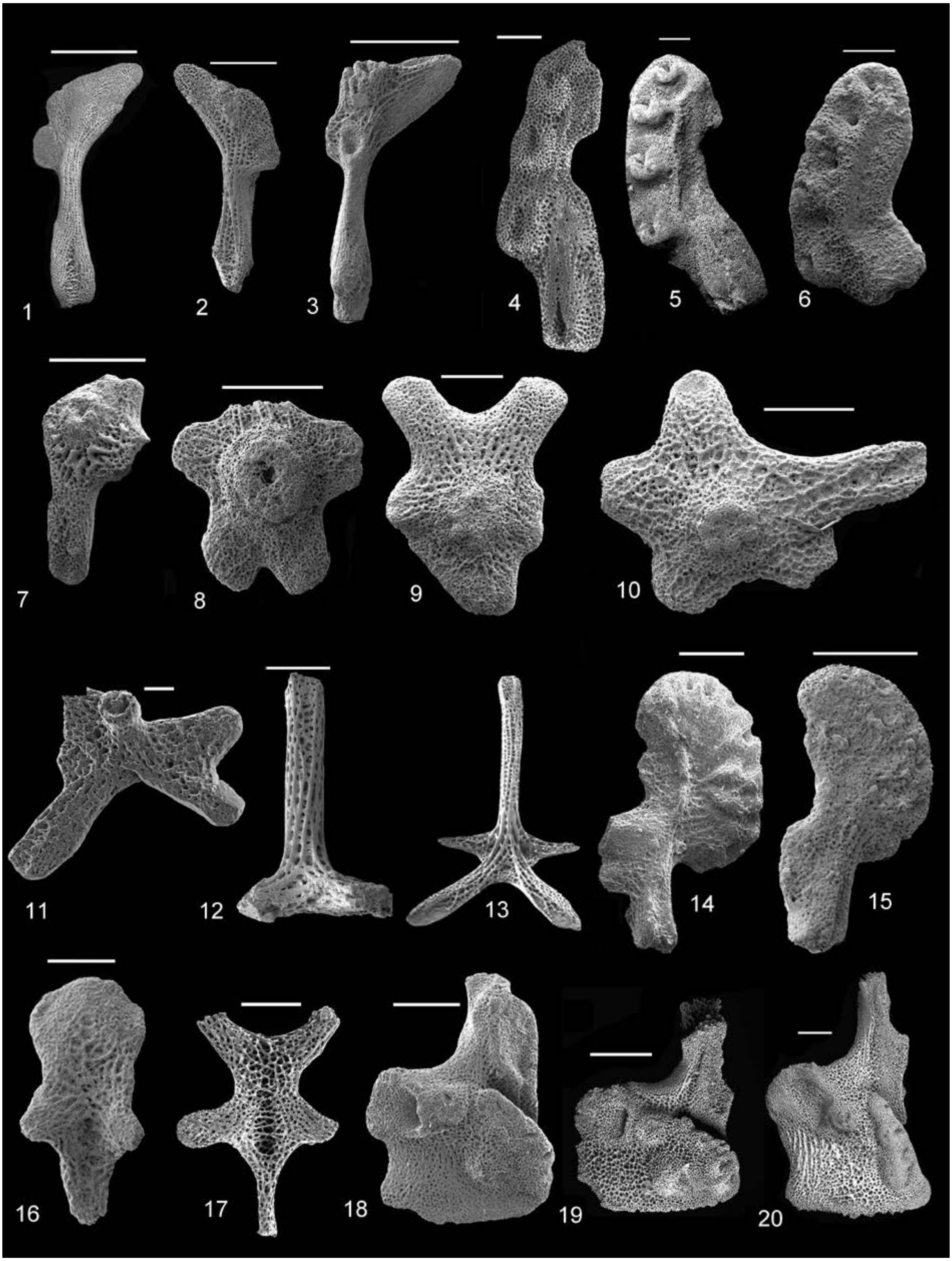
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PLATE 2

1–**10**, **12**–**14** – *Granulasterias ivoensis* gen. et sp. nov., isolated ossicles. 1, 2, 12 – external views of abacinal ossicles of unknown position, paratypes (NHMUK PI EE 18265–18267); 3–5 – superomarginals (paratypes), external view (NHMUK PI EE 18268–18270); 6, 7 – radial ossicles (paratypes), external view (NHMUK PI EE 18271, 18272); 8–10 – inferomarginals, external view, 8 is holotype (NHMUK PI EE 18264), 9, 10 are paratypes; 13 – primary abactinal ossicle from disc (paratype, NHMUK PI EE 18273); 14 – madreporite, fused with primary interradial and two adjacent ossicles (paratype, NHMUK PI EE 18274).

11, **15**–**17** – undescribed asteriid or stichasterid, isolated ossicles. 11 – superomarginal; 15–17 – abactinal view of radial ossicles (NHMUK PI EE 18383–18385).

18–**21** – Forcipulatida *incertae sedis*. 18 – radial view of oral ossicle (NHMUK PI EE 18386); 19 – actinal view of circumoral ossicle (NHMUK PI EE 18387); 20 – distal, oblique view of terminal ossicle (NHMUK PI EE 18388); 21 – actinal view of ambulacral ossicle (NHMUK PI EE 18389).

All specimens are from the upper lower Campanian at Ivö Klack, southern Sweden.

Scale bars equal 0.5 mm.

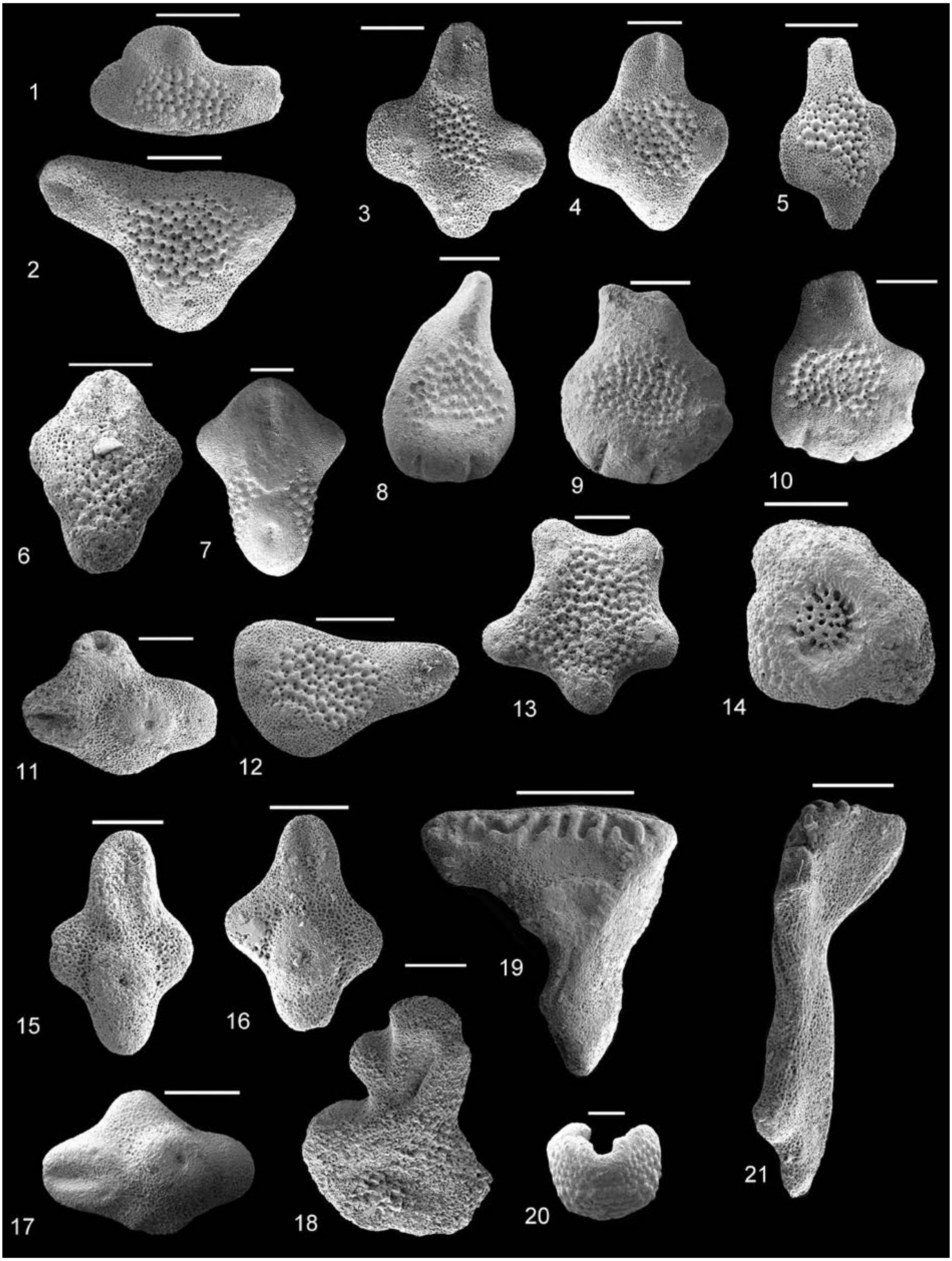
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PLATE 3

1–**9** – *Scaniasterina surlyki* gen. et sp. nov. 1–3 – abactinal ossicles in abactinal view; 1 – holotype (NHMUK PI EE 18277); 2, 3 – paratypes (NHMUK PI EE 18278, 18279); 4–9 – distal abactinal or actinal ossicles in external views (paratypes, NHMUK PI EE 18280–18285).

10 – *Tremaster mirabilis* Verrill, 1879, portion of abactinal surface to show large, imbricating abactinal ossicles.

11, **12** – *Stegnaster inflatus* (Hutton, 1872), in abactinal and actinal views, respectively.

13, **14** – astropectinid superomarginal (NHMUK PI EE 18377).

15–**18** – *Astropecten erectus* sp. nov., inferomarginal ossicles. 15, 16 – paratypes, in interradial view (NHMUK PI EE 18287, 18288); 17, 18 – holotype, in lateral and interradial views, respectively (NHMUK PI EE 18286).

19–**21** – *Lophidiaster pygmaeus* Spencer, 1913, superomarginals, in abactinal view (NHMUK PI EE 18378–18380).

22–**25** – *Coulonia* sp. 22, 23 – inferomarginal in actinal (22) and distal/proximal views (23) (NHMUK PI EE 18381); 24, 25 – superomarginal in abactinal (24) and (25) interradial views, respectively (NHMUK PI EE 18382).

Figures 1–9 and 13–25 are from the upper lower Campanian at Ivö Klack, southern Sweden. Figure 10 is from present day of the western Pacific. Figures 11, 12 are from the present day of New Zealand.

Scale bars equal 10 mm (10–13), 5 mm (1–9) and 1 mm (14–25).

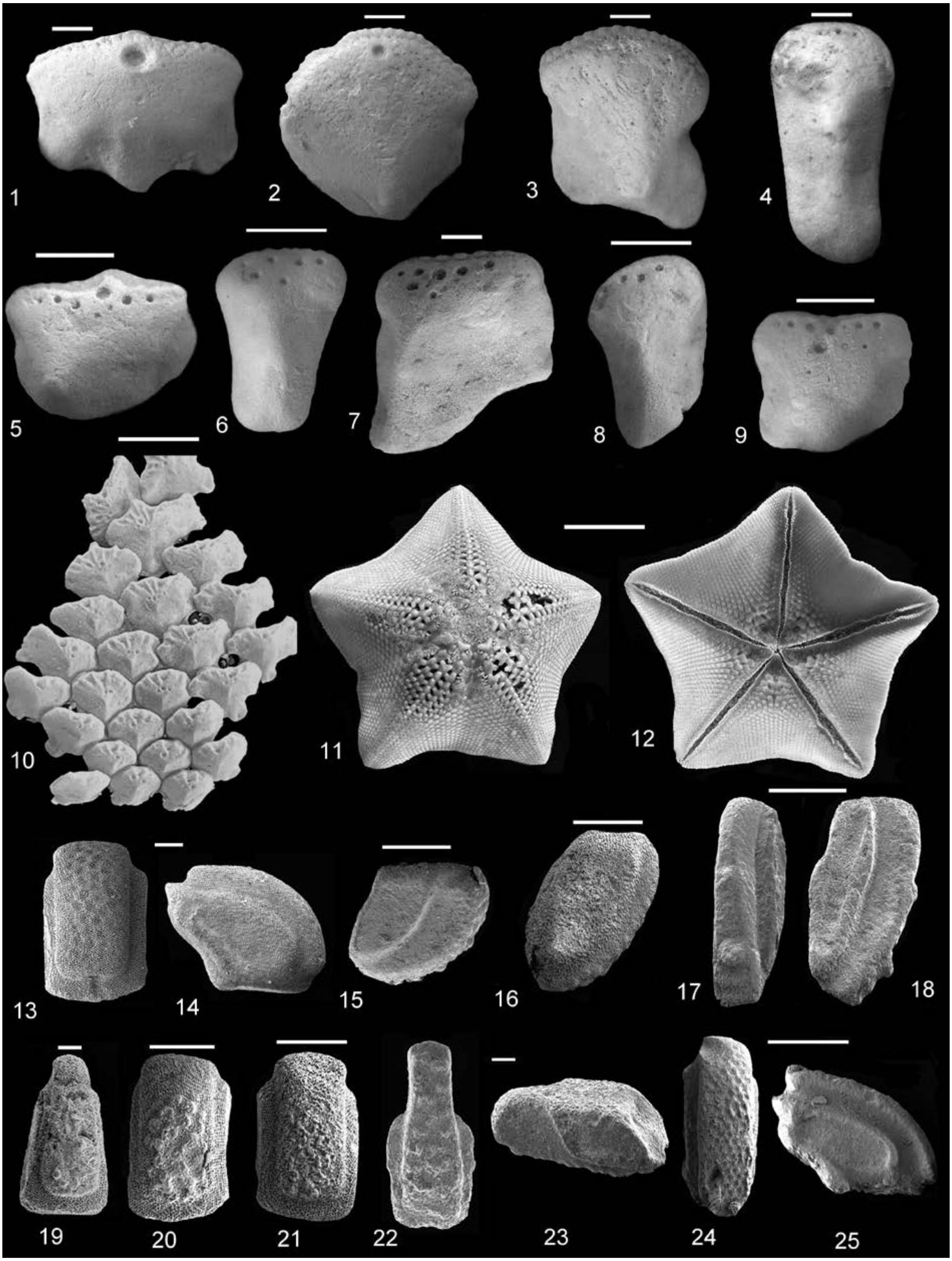
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PLATE 4

1–**7**, **12**, **13** – *Nymphaster macrogranularis* sp. nov., isolated marginal osicles. 1 – interradial marginal pair, in interradial view (paratypes, NHMUK PI EE 18300, 18301); 2 – median superomarginal, in abactinal view (holotype, NHMUK PI EE 18299); 3 – interradial inferomarginal, in actinal view (paratype, NHMUK PI EE 18302); 4, 5 – distal inferomarginal, in actinal and proximal views, respectively (NHMUK PI EE 18303); 6, 7 – median superomarginal, in proximal/distal and abactinal views, respectively (paratype, NHMUK PI EE 18304); 12 – superomarginal from base of radius, in abactinal view (paratype, NHMUK PI EE 18305); 13 – distal inferomarginal, in proximal view (paratype, NHMUK PI EE 18306).

8–**11**, **14**–**16** – *Nymphaster minigranularis* sp. nov., isolated marginal ossicles. 8 – interradial marginal pair, in proximal/distal view (paratypes, NHMUK PI EE 18292, 18293); 9–11 – median superomarginals, in abactinal view; 9, 10 are paratypes (NHMUK PI EE 18294, 18295), 11 is holotype (NHMUK PI EE 18291); 14, 15 – superomarginal, from base of arm, in proximal (14) and abactinal (15) views (NHMUK PI EE 18297); 16 – median inferomarginal in proximal/distal views (paratype, NHMUK PI EE 18296).

17 – ?Pseudarchasteridae, median superomarginal in proximal/distal view (NHMUK PI EE 18298).

18, **19** – *Nymphaster arenatus* Sladen, 1889, in abactinal and actinal views, respectively.

Figures 1–17 are from the upper lower Campanian at Ivö Klack, southern Sweden. Figures 18, 19 are from the present day of the North Atlantic.

Scale bars equal 10 mm (18, 19) and 5 mm for all others.

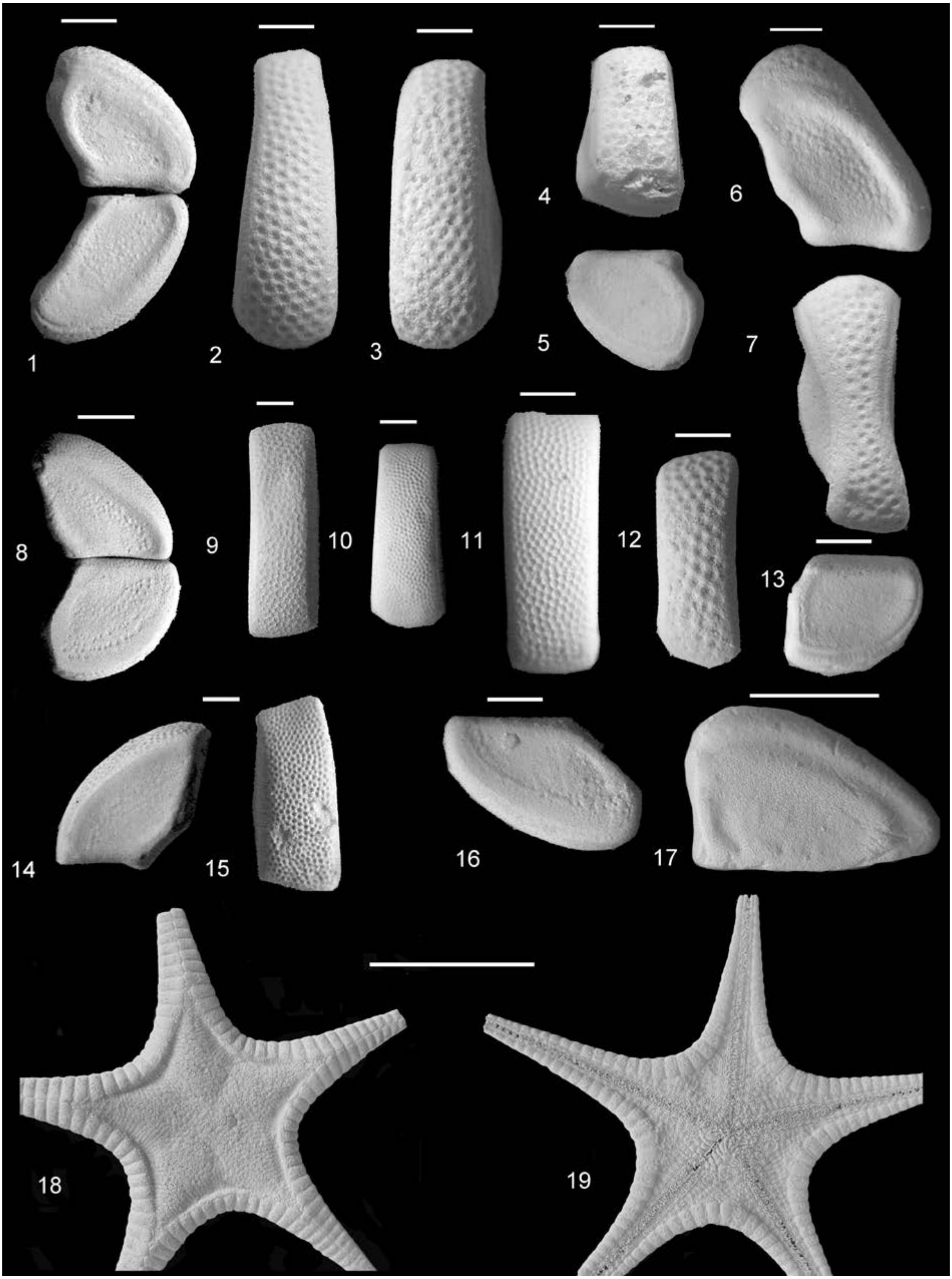
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PLATE 5

1–**4** – *Metopaster asgaardae* sp. nov. 1, 2 – ultimate superomarginal, in lateral and abactinal views, respectively (holotype, NHMUK PI EE 18308); 3, 4 – median superomarginal, in abactinal and interradial views, respectively (paratype, NHMUK PI EE 18309).

5–**7** – *Metopaster elegans* Gale, 1987a, isolated marginals. 5 – median superomarginal, in lateral view, the original of Gale (1987a, pl. 8, fig. 24; NHMUK PI EE 54273); 6, 7 – ultimate superomarginal, in lateral and abactinal views, respectively (NHMUK PI EE 18342).

8–**15** – *Metopaster calcar* Spencer, 1913, isolated marginal ossicles. 8, 9 – large ultimate superomarginal, in lateral and abactinal views, respectively (NHMUK PI EE 18343); 10, 11 – median superomarginal, in abactinal and proximal/distal views, respectively (NHMUK PI EE 18344); 12 – ultimate superomarginal, in abactinal view (NHMUK PI EE 18346); 13 – ultimate inferomarginal, in lateral view (NHMUK PI EE 18345); 14, 15 – median inferomarginal, in actinal and proximal views, respectively (NHMUK PI EE 18347).

16 – sphaerasterid adambulacral, in proximal/distal view (NHMUK PI EE 18348).

17, **18** – *Valettaster* sp., abactinal ossicles in oblique view (NHMUK PI EE 18349, 18350).

All specimens are from the upper lower Campanian at Ivö Klack, southern Sweden.

Scale bars equal 0.5 mm (17), 1 mm (18) and 5 mm for all others.

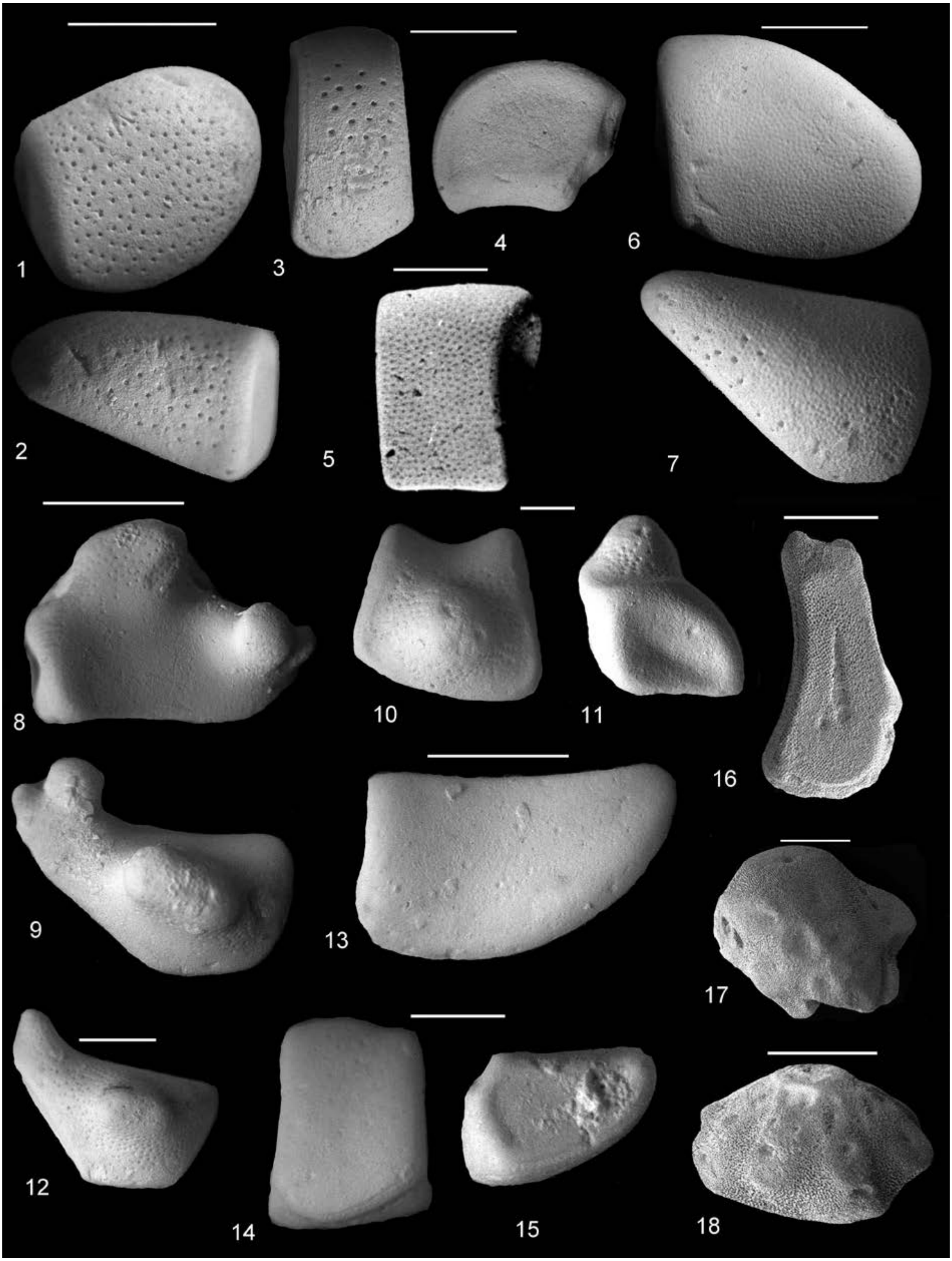
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PLATE 6

1, **2** – *Metopaster* sp., in abactinal and actinal views, respectively.

3–**6**, **9**–**11** – *Weitschataster tamarae* (Gale, 1987a). 3, 5 – median superomarginals, in abactinal view (NHMUK PI EE 18352, 18353); 4, 6 – inferomarginals, in actinal view (NHMUK PI EE 18354, 18355); 9, 10 – ultimate superomarginals, in abactinal and actinal views, respectively (NHMUK PI EE 18356, 18357); 11 – interradial profile of supero-/inferomarginal pair (NHMUK PI EE 18358, 18359).

7, **8**, **12**–**16** – *Rugometopaster rugissimus* (Gale, 1987a). 7 – abactinal view of median superomarginal (NHMUK PI EE 18360); 8 – abactinal view of ultimate superomarginal (NHMUK PI EE 18361); 12 – actinal view of median inferomarginal (NHMUK PI EE 18362); 13 – actinal view of ultimate inferomarginal (NHMUK PI EE 18363); 14 – interradial profile of supero-inferomarginal pair (NHMUK PI EE 18364, 18365); 15 – abactinal view of ultimate inferomarginal (NHMUK PI EE 18366); 16 – actinal view of ultimate superomarginal (NHMUK PI EE 18367).

17–**22** – *Haccourtaster liticola* Gale and Jagt, 2025. 17 – superomarginal frame in abactinal view, reconstructed from isolated marginals (NHMUK PI EE 18200, 18211); 18 – inferomarginal frame from one side of disc, reconstructed from isolated marginals (NHMUK PI EE 18212–18215); 19 – abactinal view of median superomarginal (holotype, NHMUK PI EE 18199); 20 – inferomarginal in actinal view (paratype, NHMUK PI EE 18217); 21 – abactinal view of ultimate superomarginal (paratype, NHMUK PI EE 18216); 22 – interradial view of inferomarginal-superomarginal pair (paratypes, NHMUK PI EE 18218, 18219).

23–**26** – *Metopaster bromleyi* Gale, 1987a. 23, 24 – ultimate superomarginal, in lateral and abactinal views, respectively, the original of Gale (1987a, pl. 2, fig. 16; holotype, NHMUK PI EE 54194); 25, 26 – median superomarginal, in abactinal and median views, respectively, the original of Gale (1987a, pl. 2, figs 14, 15; NHMUK PI EE 54192, 54193).

Figures 1, 2 are from the present day of the Philippines. Figures 3–26 are from the upper lower Campanian at Ivö Klack, southern Sweden.

Scale bars equal 10 mm (1, 2), 2 mm (3–16, 23–26) and 1 mm (17–22).

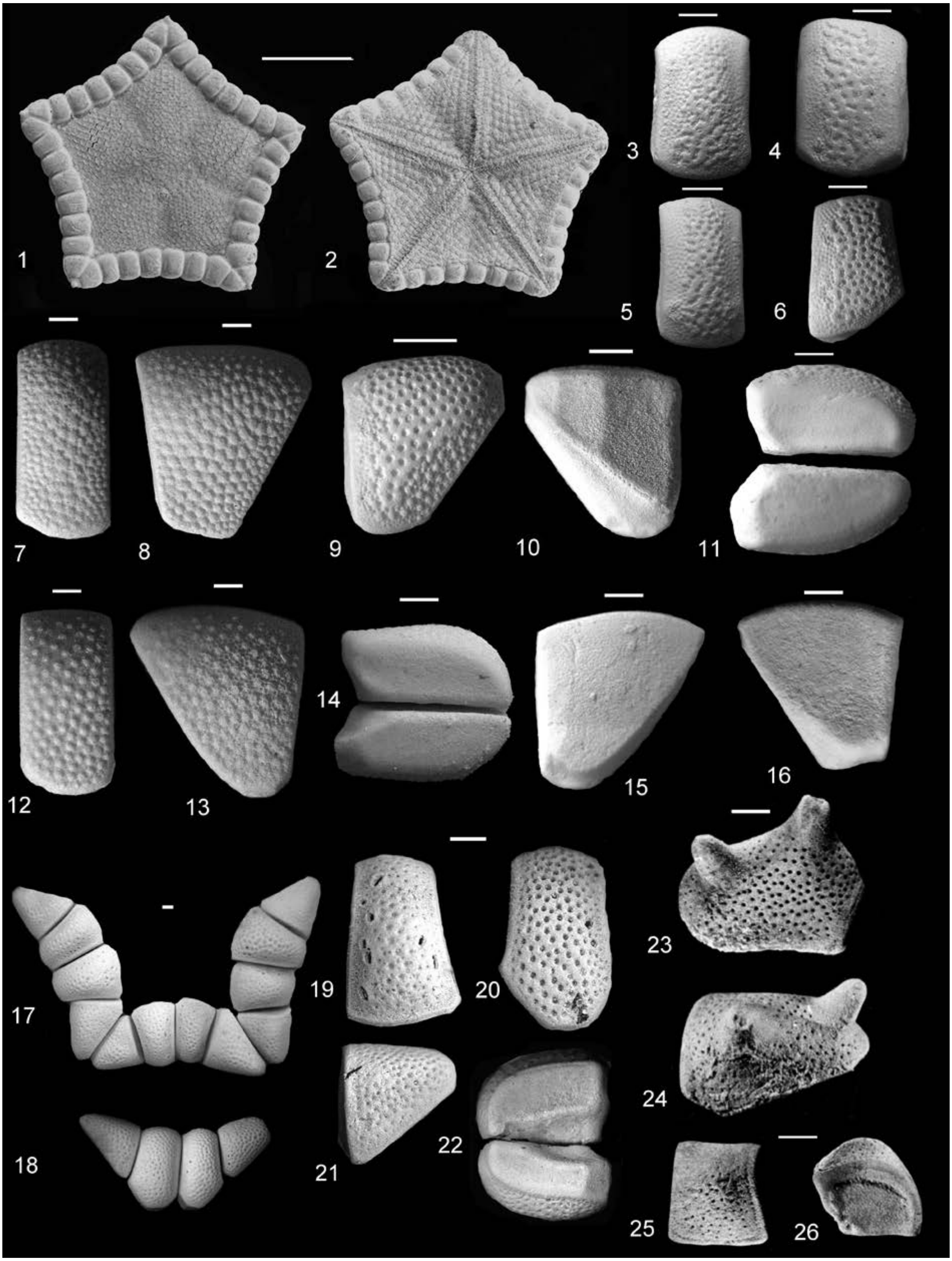
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PLATE 7

1–**7** – *Pycinaster christenseni* sp. nov. 1 – median superomarginal, in lateral view (holotype, NHMUK PI EE 18368); 2, 3 – superomarginal in distal and lateral views, respectively (paratype, NHMUK PI EE 18369); 4 – superomarginal in lateral view (paratype, NHMUK PI EE 18370); 5 – inferomarginal in interradial view (NHMUK PI EE 18371); 6, 7 – median superomarginal in lateral and interradial views, respectively (paratype, NHMUK PI EE 18372).

8 – *Pycinaster magnificus* Spencer, 1913, lateral view of reconstructed interradial marginals (NHMUK PI EE 18339).

9–**15** – *Ivoaster soerensenae* gen. et sp. nov., isolated marginal ossicles. 9, 10, 12 – lateral view of superomarginals; 12 is the holotype (NHMUK PI EE 18375), 9, 10 are paratypes (NHMUK PI EE 18376, 18377); 11 – interradial profile of supero- and inferomarginal pair (paratype, NHMUK PI EE 18380, 18381); 13–15 – actinal view of inferomarginals (paratypes, NHMUK PI EE 18378, 18379, 18379a).

Figures 1–7 and 9–15 are from the upper lower Campanian at Ivö Klack, southern Sweden. Figure 8 is from the lower Campanian at East Harnham, Wiltshire, UK.

Scale bars equal 10 mm (8) and 5 mm for all others.


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PLATE 8

1–**3** – *Manfredaster bulbiferus* (Forbes, 1848). 1 – abactinal view of well-preserved individual (NHMUK E 4344); 2, 3 – distal arm, reconstructed from associated ossicles, in abactinal and transverse views, respectively (NHMUK PI EE 18375).

4–**14** – *Manfredaster graveseni* sp. nov., isolated ossicles. 4 – median marginal (paratype, NHMUK PI EE 18311); 5 – distal inferomarginal, oblique actinal view (paratype, NHMUK PI EE 18312); 6 – two distal superomarginals and a radial ossicle in distal view (paratypes, NHMUK PI EE 18313–18315); 7 – primary interradial ossicle, abactinal view (paratype, NHMUK PI EE 18316); 8 – primary interradial ossicle from madreporic interradius, in abactinal view (paratype, NHMUK PI EE 18317); 9– primary abactinal ossicle (paratype, NHMUK PI EE 18318); 10, 14 – marginals from median part of arm in oblique distal view (paratypes, NHMUK PI EE 18319, 18320); 11, 12 – distal superomarginals in lateral view (paratypes, NHMUK PI EE 18321, 18322); 13 – abactinal ossicle (paratype, NHMUK PI EE 18323).

Figure 1 is from the upper Coniacian or lower Santonian at Bromley, Kent, UK. Figures 2, 3 are from the lower Santonian at Kingsgate, Kent, UK. Figures 4–14 are from the upper lower Campanian at Ivö Klack, southern Sweden.

Scale bars equal 10 mm (1), 5 mm (2, 3) and 2 mm for all others.

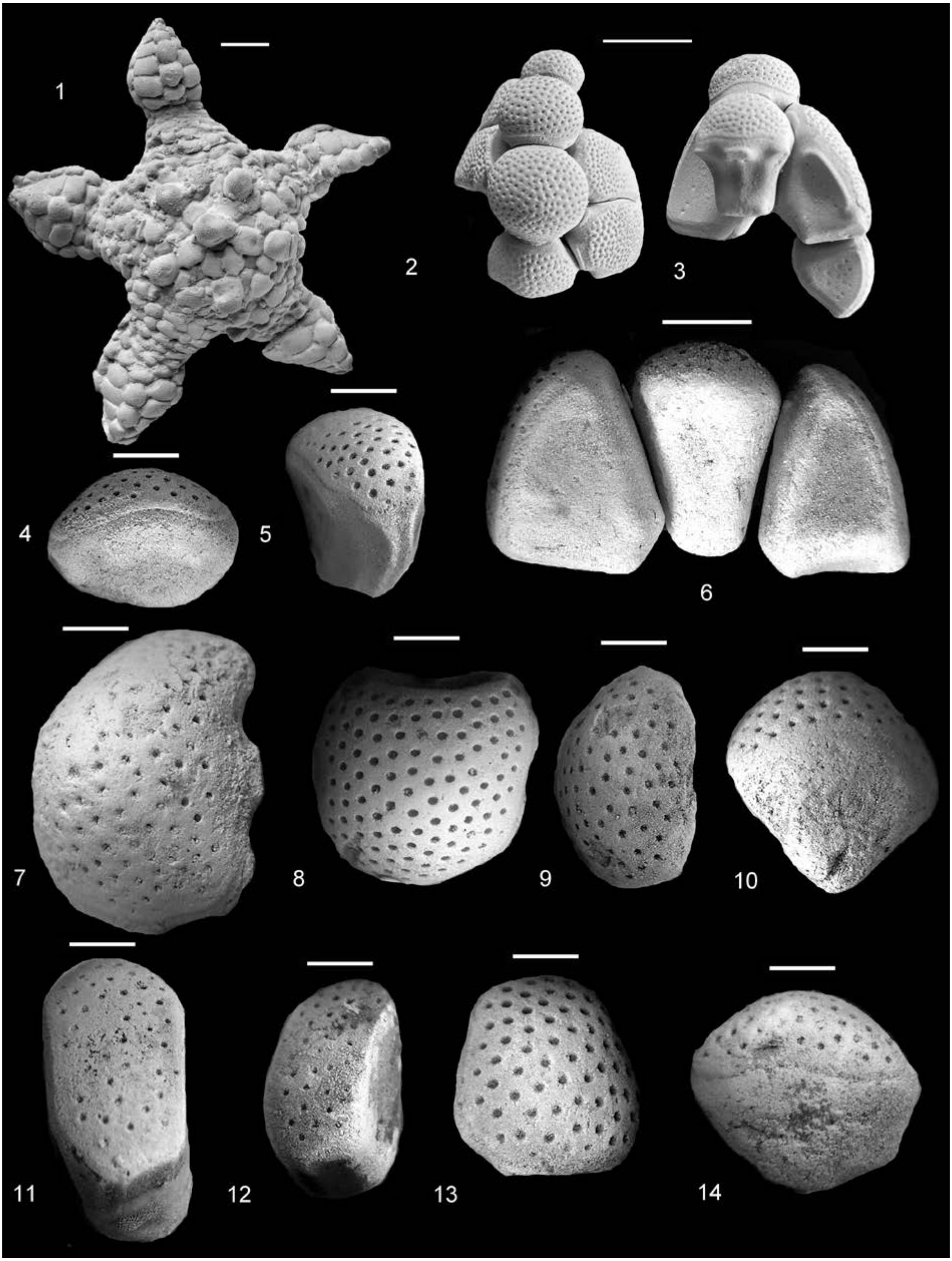
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PLATE 9

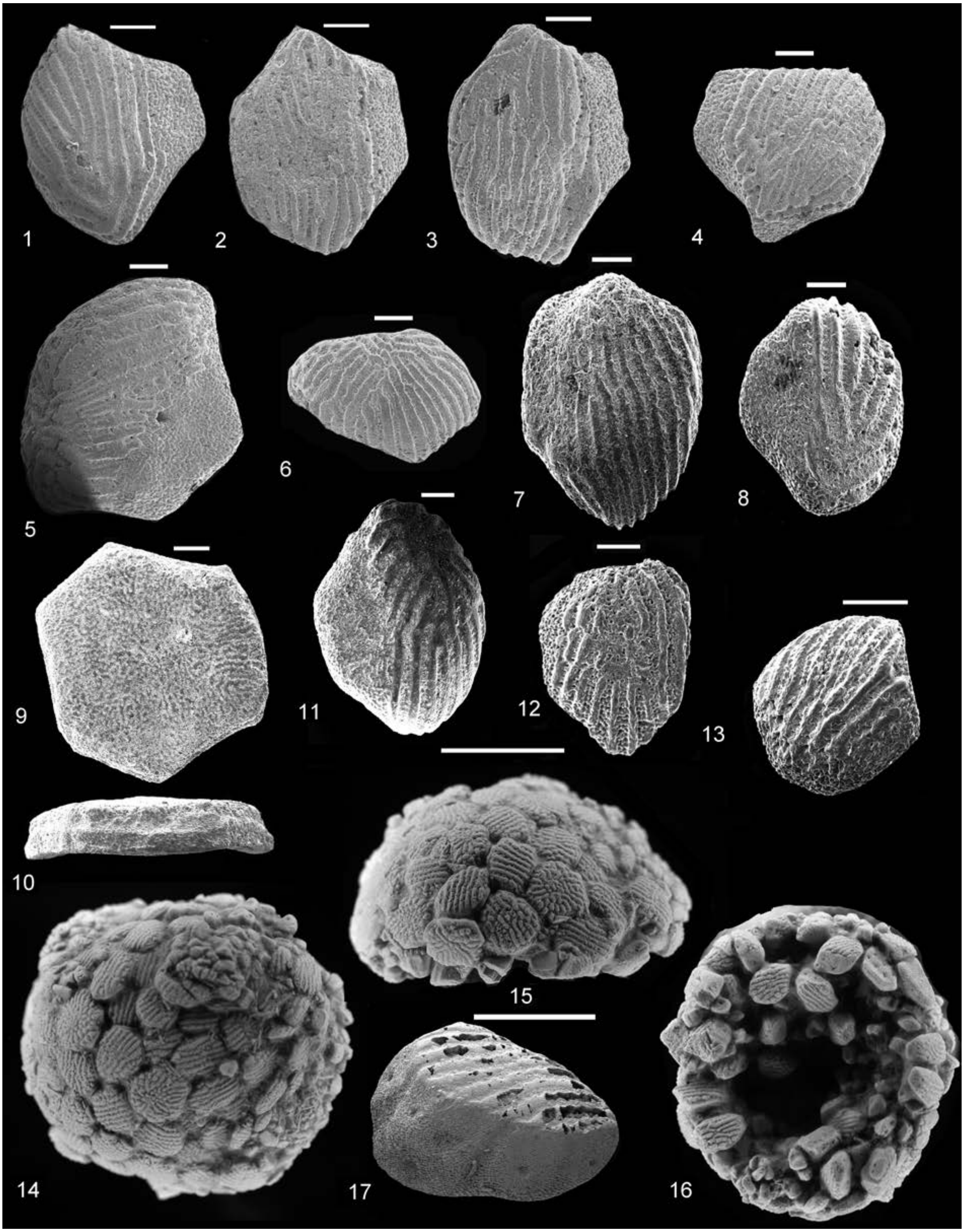
1–**8**, **11**–**13** – *Vectisaster enigmaticus* gen. et sp. nov. Isolated ossicles, in external view. 1 is the holotype (NHMUK PI EE 18327), 2–8 and 11–13 are paratypes (NHMUK PI EE 18328–18338).

9, **10** – undescribed sphaerasterid, isolated abactinal ossicle (NHMUK PI EE 18376).

14–**17** – *Rugosphaeraster ruegenensis* Gale, 2021; 14–16 – complete individual, in abactinal, lateral and actinal views, respectively, the original of Neumann *et al.* (2023, fig. 42A–C); 17 – abactinal ossicle in oblique view, the original of Gale (2021, fig. 26N; NHMUK PI EE 17698).

Figures 1–8 are from the lower Campanian, *Gonioteuthis quadrata* belemnite Zone at Whitecliff, Isle of Wight, UK. Figures 14–16 are from the lower Campanian, *pilula/senonensis* Zone at Misburg, Germany. Figures 9–13, 17 are from the upper lower Campanian at Ivö Klack, southern Sweden.

Scale bars equal 10 mm (14–16), 1 mm (17) and 0.3 mm for all others.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